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Systematics of the melicerititid cyclostome bryozoans; introduction and the genera *Elea*, *Semielea* and *Reptomultelea*

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CONTENTS

Synopsis. The Family Eleidae, whose species are commonly referred to as melicerititids, is an unusual clade of cyclostome bryozoans with operculate zooids, a homoplasy shared with cheilostomes. Melicerititids range from the Barremian to the Palaeocene and are mostly European in geographical distribution. They are especially abundant and diverse in some Cenomanian-Campanian deposits of England, France and Germany. This paper is the first part of an intended comprehensive systematic revision of melicerititid species. Following a brief account of the history of melicerititid research and a review of their morphology, the main part of the paper describes 36 species belonging to the three fixed-walled genera (*Elea*, *Semielea* and *Reptomultelea*) with lamellar colony forms. Almost all of these species have been studied with the aid of scanning electron microscopy, and most of the type material has been re-examined and lectotypes chosen when necessary. The following 20 species are new: *Elea elegantula*, *E. flabellata*, *E. mackinneyi*, *E. pseudolamellosa*, *E. subhexagona*, *E. viskovae*, *E. whiteleyi*, *Reptomultelea acclivata*, *R. auris*, *R. bituberosa*, *R. convexa*, *R. goldfussi*, *R. levinseni*, *R. matutina*, *R. mitrus*, *R. parvula*, *R. pegma*, *R. pseudopalpebrosa*, *R. reedi* and *R. scanica*. *Reptomultelea betusora* is proposed as a new name for *R. tuberosa* (Reuss), a junior homonym of *R. tuberosa* d'Orbigny. Keys are provided for the identification of melicerititid genera, and for species of *Elea* and *Reptomultelea*.

INTRODUCTION

This is the first of a planned series of papers intended to provide a complete systematic account of the cyclostome bryozoan family Eleidae, commonly referred to as 'melicerititids' (Family Melicerititidae) and occasionally as 'operculate cyclostomes'. Melicerititids range from the Barremian Stage of the Lower Cretaceous to the Danian Stage of the Palaeocene, a duration of over 60 MA. Almost all species come from localities in Europe; melicerititids are presently unrecorded from the Americas, Africa, Antarctica and Australasia. They are important constituents of many bryozoan faunas, especially in the Upper Cretaceous of western Europe. However, melicerititids have never been comprehensively monographed, although Levinsen (1912) did revise many of the commoner species in the only major publication devoted to the group.

Melicerititids were chosen for detailed study for three principal reasons:

1. They clearly constitute a monophyletic group (clade), defined by the possession of a calcified zooidal operculum, and are therefore one of very few unequivocal clades which can be currently distinguished among cyclostome bryozoans or indeed stenolaemates in general. Questions concerning evolutionary patterns can be addressed with more clarity in monophyletic groups (see Smith, in press).
2. Melicerititids have a greater number of morphological characters for use in taxonomy than most other cyclostomes, principally because of the wide variety of apertural shapes and zooidal polymorphs they possess.
3. The operculum and avicularium-like polymorphs of melicerititids evolved in parallel with those of contemporaneous cheilostomes, providing an opportunity for comparative study of morphological and taxonomic diversification in two distantly-related groups of bryozoans.

These factors mean that melicerititids are a good target group among stenolaemate bryozoans for studies of evolutionary patterns; for example, evolutionary trends, convergent evolution, and patterns of extinction and radiation.

HISTORY OF RESEARCH

The early history of research on melicerititids was fully chronicled by Levinsen (1912) and will only be summarized here. The first melicerititid species to be formally named was *Ceriopora gracilis* Goldfuss, 1826, from the Cenomanian of Essen in Germany. This species was subsequently assigned by Roemer (1840) to *Meliceritites*, the first genus to be proposed for a melicerititid. Roemer also assigned to his genus two other Cretaceous species, *Ceriopora roemeri* v. Hagenow, 1839 and a new species, *Meliceritites porosa*. The genus name *Meliceritites* was derived from the cheilostome genus *Melicerita* on account of their superficial similarity, notably in the hexagonal frontal shapes of the zooids.

The history of higher classification of the melicerititids began in 1851 when v. Hagenow referred *Meliceritites* (as *Escharites*) and *Inversaria* (now known to be a cheilostome, see Voigt & Williams, 1973; Voigt, 1974) to his division Salpingina, claiming to have identified opercula in both genera. Levinsen (1912) was probably correct in doubting v. Hagenow's claim: one of the species (*Escharites [Filicea] velata* v. Hagenow) in which opercula were supposedly seen by v. Hagenow lacks opercula but has terminal diaphragms that could have been mistaken for opercula. A year later d'Orbigny (1852) founded a division – Centrifuginés operculinés – for two of his new families, Eleidae and Myriozoumidae, making clear from the diagnosis that he had observed true opercula. While the Eleidae is nowadays the accepted family for *Meliceritites* and related genera of operculate cyclostomes, including the type genus *Elea*, the Myriozoumidae is recognized as a family of ascophoran cheilostomes.

Hamm (1881) included *Meliceritites*, together with two non-operculate cyclostomes (*Stigmatopora* Hamm and *Cyrto-*

pora Hamm), in the Stigmatoporina, a highly artificial division not adopted by later workers. Another disregarded group is the 'Typus' Metopoporina under which Marsson (1887) united the Eleidea [sic] and Ceidea [sic] based on their trumpet-shaped zooids (the remaining cyclostomes were placed in the 'Typus' Solenoporina). Despite the disuse of Metopoporina, the practice of grouping together these two families has persisted, notably in the *Treatise* (Bassler, 1953). Pergens (1890) referred the Eleidae to his Melicertitina.

Whereas Hamm (1881), Marsson (1888) and Pergens (1890) denied the presence of an operculum in melicerititids, Waters (1891) thought that only a chitinous operculum might have been present. Waters did, however, recognize the similarity between the eleozooids of melicerititids and cheilostome avicularia. Gregory (1899) confused opercula with terminal diaphragms (like several of his predecessors), but acknowledged the existence of 'avicularia', and observed brood chambers ('gonoecia' and 'gonocysts') in melicerititids. He also considered ceid cyclostomes to be merely worn specimens of melicerititids in which the frontal wall has been lost.

D'Orbigny's (1852) recognition of opercula was reaffirmed by Levinsen (1902). Lang (1906) very briefly revised the encrusting melicerititids, but his key to their generic identification is flawed in several respects. Thirty species and three varieties of melicerititids were described by Levinsen (1912) in a short monograph remarkable for the accuracy of its detailed observations and careful interpretations. Few advances have been made in understanding melicerititids since Levinsen's fundamental paper, although some papers have included systematic descriptions or figures of melicerititid species, notably those of Canu & Bassler (1922, 1926), Voigt (1924, 1928, 1951, 1953, 1960, 1962, 1967, 1973, 1975*a*, 1975*b*, 1981, 1983, 1985*a*, 1985*b*, 1989), Prantl (1938), Viskova (1965, 1970), Walter and coauthors (Walter 1975, 1977; Delamette & Walter, 1984; Masse & Walter, 1974; Walter & Clavel, 1979; Walter *et al.*, 1975), Brood (1972), Taylor (1987*a*, *b*), Pitt & Taylor (1990), and Favorskaja (1992).

Aspects of melicerititid morphology and palaeobiology were treated by: Boardman (in Boardman *et al.*, 1983), who reconstructed the soft tissues around the operculum; McKinney (1975), who described zooecial budding patterns of melicerititids and other dendroid stenolaemates; Taylor (1982), who described probable predatory borings in melicerititid zooids; and Taylor (1986*a*), who reviewed polymorphism in the group. More recently, Schäfer (1991) has described the gonozooids of melicerititids, and Taylor (1990) used melicerititids as an example of the application of scanning electron microscopy in bryozoology.

The systematic position of melicerititids within the Cyclostomata has received scant attention. Bassler (1953), in the bryozoan *Treatise*, grouped the Eleidae with the Ceidae (= Semiceidae Buge, 1952), placing the two families in the Suborder Salpingina. Viskova and Morozova (1988) and Viskova (1992) published an unorthodox classification which recognized three post-Palaeozoic orders of stenolaemates: Tubuliporida Blainville, Cerioporida Bronn, and Melicerititida Pergens. Within the Order Melicerititida they placed the families Eleidae d'Orbigny, Melicerititidae Pergens, Semiceidae Buge and Lobosoeciidae Canu & Bassler. There is little evidence to suggest a closer relationship between melicerititids and the two latter families than between melicerititids and several other tubuliporine families. Furthermore, partitioning the melicerititids between two families (Eleidae and Melicerititidae) rather than uniting them in a single family (Eleidae) implies an understanding of relationships between genera which is currently lacking; for example, it is unclear whether *Reptomultelea* (even if monophyletic) is more closely related to *Elea* than to *Meliceritites* (see p. 47).

General morphological comparison suggests that the sister group of melicerititids probably lies among non-operculate tubuliporine cyclostomes, notably *Collapora* and its relatives, which are traditionally assigned to the Family Multisparsidae (= Macroeciidae). Pending a comprehensive phylogenetic study, the Eleidae are here placed within the Suborder Tubuliporina Busk, 1852, although it is acknowledged that this suborder as currently understood is almost certainly paraphyletic.

MORPHOLOGY

The principal morphological characters observed in melicerititids are summarized in Table 1. Key features of melicerititid morphology are discussed below, with important terminology printed in **bold**, and the external appearance of zooidal polymorphs is depicted diagrammatically in Figure 1. It must be emphasized that the text below is not intended as a comprehensive account of all of the morphological variations found in melicerititids.

Colony-form

Despite the unusual morphology of the zooids in melicerititids, the range of colony-forms within the family is typical of

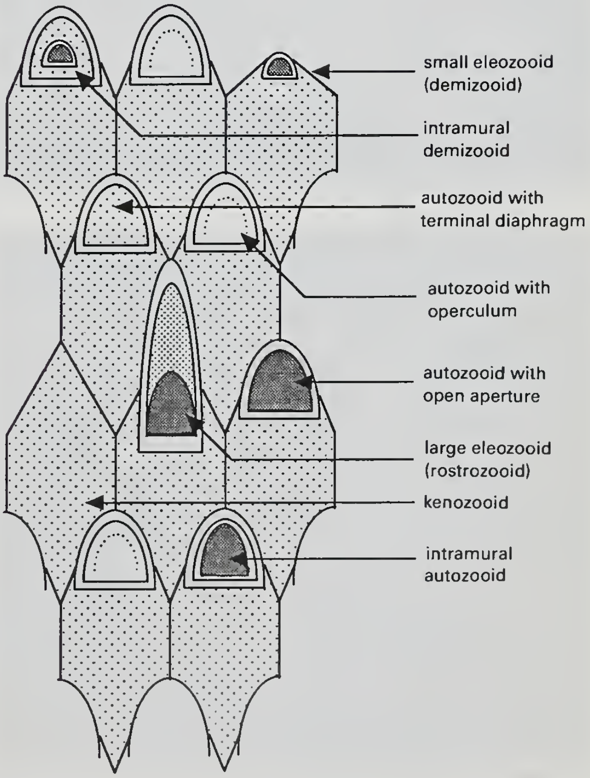


Fig. 1 Diagrammatic illustration of external zooidal morphology and polymorphism in melicerititid cyclostomes.

Table 1 Principal morphological characters of melicerititids.

Colony
a. colony-form (encrusting, multilamellar, vinculariform without axial canal, vinculariiform with axial canal, adeoniform, eschariform, cavariiform)
b. branch width/colony layer thickness
c. overgrowths (presence, abundance, polymorph type of pseudoancestrula)
d. base (extent, ancestrula, zone of astogenetic change)
e. organization (fixed-walled, free-walled, mixed)
f. zooid arrangement (whorls, quincunx, irregular, one side of branch only)

Autozooids
a. frontal length
b. frontal width
c. frontal elongation (length:width ratio)
d. frontal shape
e. boundary wall
f. aperture length
g. aperture width
h. aperture elongation (length:width ratio)
i. aperture shape
j. size of aperture relative to frontal area
k. apertural shelf
l. hinge teeth/bar
m. abundance of in-situ opercula
n. opercular pseudopore number and distribution
o. surface ornament of opercula
p. opercular sclerites
q. terminal/subterminal diaphragms (abundance, placement, pseudopores, perforations)
r. intramural buds

Eleozooids
a.–r. of autozooids, and:
s. affect on surrounding az (e.g. overgrowth, displacement)
t. rostral platform

Kenozooids and cancelli
a. distribution
b. surface features

Gonozooids
a. abundance
b. total frontal length
c. dilated frontal wall length
d. frontal width
e. frontal shape
f. inflation
g. ooeciopore length
h. ooeciopore width
i. ooeciopore shape (length:width ratio)
j. atrial ring
k. floor morphology

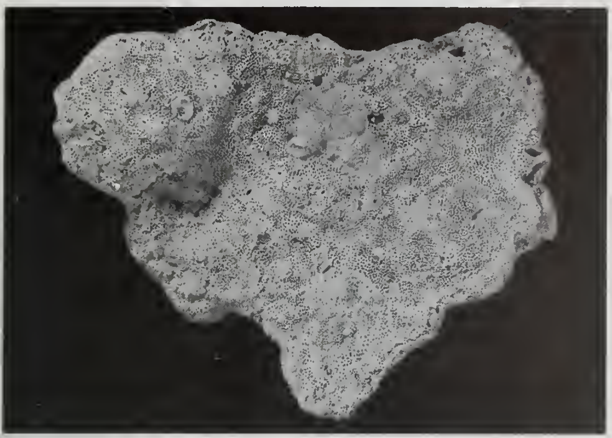
that encountered in many cyclostome groups. The following main colony-forms occur, in approximate order of frequency: erect dendroid (Figs 3, 5–7), encrusting multiserial and multilamellar (Figs 2,4, 181–184), erect bifoliate (Figs 17, 49, 87), erect tubular (Figs 110, 119, 121–123) and erect fenestrate (see Taylor 1987*a*). Common growth-forms of cyclostome bryozoans not represented among melicerititids are uniserial or pauciserial (ribbon-like) encrusting colonies, and articulated erect colonies.

All colonies begin with an encrusting base, usually attached to a hard substrate such as a shell (Figs 37, 134, 211) or pebble. However, some colonies were evidently attached to a perished organic substrate, leaving a mould bioimmuration usually in the shape of a hollow cylinder. In some cases, the edge of the original substratum was overlapped and the younger parts of the colony base grew freely over the sea-bed, becoming essentially free-lying (Fig. 183). Secondary substrates were occasionally incorporated into the bases of these free-lying colonies as they expanded across the sea-bed.

Erect growth is entirely lacking in species of *Reptomultelea* and the exclusively encrusting colonies are typically multilamellar (Fig. 4). However, the majority of melicerititid species developed erect growth from an encrusting base. Most erect colonies have subcylindrical branches, less than 2 mm in diameter, which bifurcate to give a dendroid, bushy colony (Figs 5–7) equivalent to the vinculariiform morphotype of cheilostomes. Species of *Meliceritites*, *Atagma*, *Meliceritella* and *Foricula* all have this colony-form. In most of these colonies, feeding zooids are evenly distributed around the circumference of the branches which, therefore, fall within the radial non-maculate category of McKinney (1986*a*, *b*). However, a few species with wider branches may develop raised **monticular maculae** (e.g. *Foricula aspera*). Multiple lamellar overgrowths are characteristic of many species with erect branches, particularly fixed-walled dendroid and broad bifoliate colonies. Branches of these colonies resemble the Jurassic cyclostome *Terebellaria* (Taylor, 1978) in cross-section, and may be termed 'terebellariiform'. In *Meliceritella* autozooids have a restricted distribution around the circumference of the subcylindrical branches which have a well-defined reverse or dorsal side composed of kenozooids and/or eleozooids. This colony morphotype therefore falls within the unilaminate category of McKinney (1986*a*, *b*). *Meliceritella* specimens are invariably recovered as short broken branches and it is usually uncertain whether colonies were originally bushy and three-dimensional or were almost two-dimensional planar fronds. However, scarcity of branch anastomoses suggests that most colonies were bushy with the exception of one species, *M. schneemilchae*, in which regular branch bifurcation and anastomosis in a single plane gives a fenestrate colony-form (Taylor, 1987*a*).

Less common among melicerititids are dendroid erect colonies with bilaminate branches in which zooids bud from both sides of a **median lamina** (Figs 26–27). Bilaminate colonies can have either narrow, strap-like branches which bifurcate in the plane of the budding lamina (e.g. *Elea elegantula*), or broad, foliaceous fronds which can be folded into complex corrugations or anastomosed into box-like structures (e.g. *E. lamellosa*). These occur in the fixed-walled

Figs 2–7 Colony forms in melicerititid cyclostomes. 2, multilamellar encrusting colony of *Reptomultelea sarthacensis* (d'Orbigny, 1853); EM RE 551.763.31.A711, Cenomanian, Essen, Germany; × 1·4. 3, typical assemblage of fragments of erect dendroid species; BMNH sample, Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, France; *ca* × 3. 4, worn edge of multilamellar colony of *Reptomultelea* sp. showing layering; EM RE 554. 763. 31. A745/9, Cenomanian, Essen, Germany; × 4·5. 5, erect dendroid colony of *Meliceritites dendroidea* (Keeping, 1883) embedded in a matrix of glauconitic sandstone; BMNH D3145, Aptian, Lower Greensand, Shanklin, Isle of Wight, England; × 0·8. 6, dendroid specimen of *M. dendroidea* with a densely-branched colony-form; BMNH D55269, Aptian, Faringdon Sponge Gravel, Little Coxwell Pit, Faringdon, Oxfordshire, England; × 2·2. 7, small, loosely-branched dendroid colony of *M. semiclausa* (Michelin, 1846) with a concave encrusting base of small area; BMNH D3695, Cenomanian, Le Mans, Sarthe, France; × 4·4.



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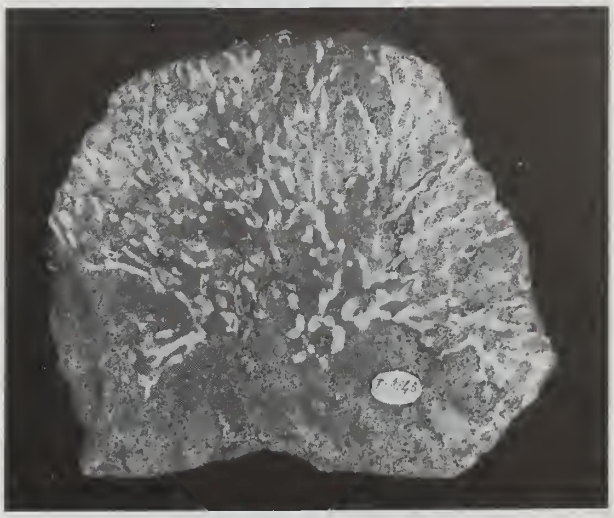

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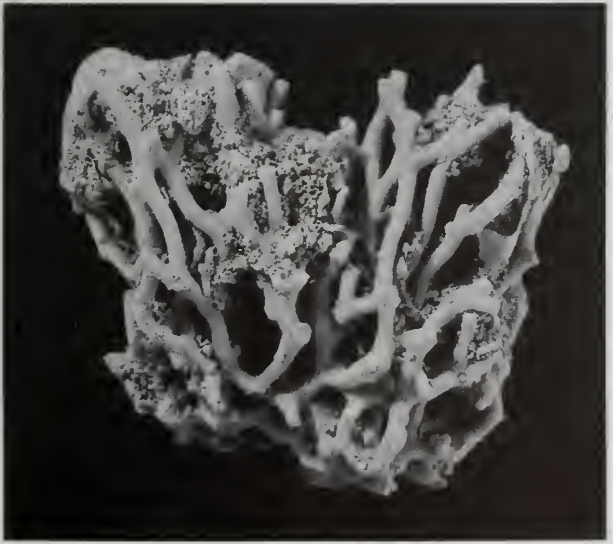

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genus *Elea* and its free-walled analogue *Biforicula*.

Consistently tubular branches characterize the genus *Semielea*. The **axial lumen** (Fig. 119) of these branches is about 1 mm in diameter, and lined by an apparent exterior wall which is transversely wrinkled and whose origin can be traced back to the basal lamina of the colony base (Fig. 122). These 'cavariiform' branches seem not to be the result of growth around a perished substratum as the walls of the lumen evidently grew freely into space and do not bioimmure a substratum. Furthermore, the lumen is occasionally divided by transverse platforms which could not have formed in a colony wrapped around a cylindrical substratum (cf. *Lopholepis radians*, see Voigt, 1982: pl. 9, figs 3–6).

Much narrower **axial canals** occur in some species of *Meliceritites* (e.g. *M. semiclausa;* see McKinney, 1975: pl. 3, fig. 3a) but appear to be formed of interior rather than exterior wall. These resemble the axial canals found in the Mesozoic non-melicerititid tubuliporine genera *Entalophora* (see Walter, 1970), *Bicoronipora* (see Walter, 1987), and *Coelospiropora* (see Voigt, 1968; Voigt & Flor, 1970; Walter, 1987), and in the late Palaeozoic cryptostome genus *Rhabdomeson* (see Blake *in* Boardman *et al.*, 1983). Axial canals of this type are of uncertain origin and function. Some may be greatly-elongated polymorphic zooids. It is possible that axial canals provided a pseudocoelomic connection of physiological value between branch growing tips and the older, more proximal zooids of the colony. Alternatively, their function may have related to the provision of a surface from which zooidal budding could occur.

Overgrowths can be found in most melicerititid species. They usually originate by intrazooecial fission (sensu Hillmer *et al.*, 1975) and subsequent eruptive budding of the newly-formed zooids onto the colony surface. Incipient overgrowths are first evident as apertures divided into an average of six chambers by radial walls arranged as spokes around an inner chamber enclosed by a ring-like wall (Figs 250, 271–272, 284). The inner chamber is apparently continuous with that of the parent zooid and develops into a **pseudoancestrula** at the centre of the overgrowth (Figs 131, 163, 179, 206–207, 212–213, 221, 225, 285). The pseudoancestrula is encircled by radially-orientated zooids originating from the surrounding chambers. A circular overgrowth with a circumferential growing edge is thus formed. Often several closely-spaced overgrowths are present and these coalesce as they grow outwards and come into contact with one another. Overgrowths are structurally distinct units and can be classified as subcolonies. Conspicuous secondary zones of astogenetic change are developed, beginning with the pseudoancestrula, which has a small aperture and little or no frontal wall. Aperture and frontal wall dimensions increase progressively through the succeeding generations of zooids. In species with high and pointed apertures (e.g. *Meliceritites gracilis* (Goldfuss)), zooids in secondary zones of change also tend to have proportionally shorter and more rounded apertures than zooids from zones of astogenetic repetition.

Skeletal organization

The major structural walls of bryozoan colonies can be categorized as basal walls, vertical walls and frontal walls. In all cyclostome bryozoans basal walls are apparently exterior walls, secreted from one side only, and include a calcified layer between the secretory epithelium and cuticle. Vertical walls and frontal walls may be with or without calcified layers. Three basic skeletal organizations (see Taylor & Larwood, 1990: fig. 10.6 for a simplified representation, and Boardman *in* Boardman *et al.*, 1983 for more detailed explanations of the latter two organizations) can be recognized according to which of these walls have calcification:

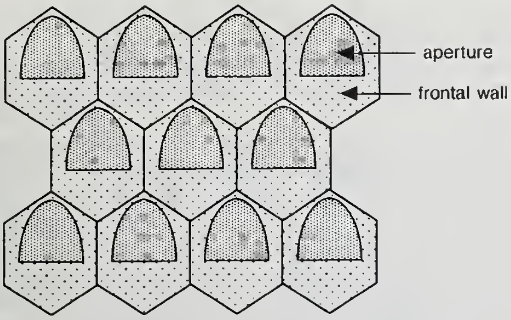
1. **Corynotrypid**. Known only in the Palaeozoic Family Corynotrypidae, this organization is characterized by calcified frontal exterior walls but non-calcification (or absence) of vertical walls.
2. **Fixed-walled**. Previously termed single-walled (Borg, 1926), fixed-walled organization has calcification of both interior vertical walls and exterior frontal walls. Frontal walls are fixed to the ends of the vertical walls.
3. **Free-walled**. Previously termed double-walled (Borg, 1926), here only the interior vertical walls are calcified. The frontal exterior wall remains uncalcified and is free of the vertical walls, enclosing a hypostegal pseudocoel between itself and the ends of the vertical walls.

Skeletal organization has been employed in the subordinal division of cyclostomes: two suborders (Tubuliporina and Articulata) are essentially fixed-walled, and three suborders (Cerioporina, Cancellata and Rectangulata) essentially free-walled. However, it is becoming increasingly clear that the taxonomic distinction between fixed- and free-walled cyclostomes is more complex. For example, the gonozooids of otherwise free-walled cerioporines are fixed-walled (e.g. Schäfer, 1991); individual branches of *Cinctipora elegans* can show alternations of free- and fixed-walled autozooids (Boardman *et al.*, 1992); and Boardman (1975) has described fixed-walled organization in a species of the normally free-walled genus *Heteropora*.

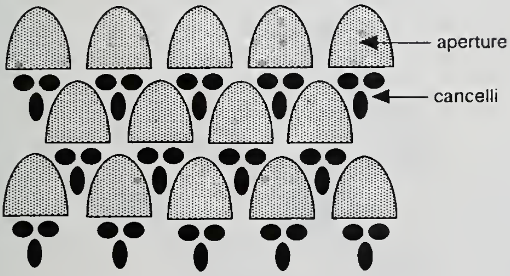
Melicerititids provide another example of the mixing of skeletal organizations. In all species for which they have been described, gonozooids are fixed-walled, whereas autozooids (and eleozooids) can be either fixed- or free-walled. Two melicerititid genera (*Foricula* and *Biforicula*) have free-walled autozooids, but the remaining genera possess fixed-walled autozooids. The areas between autozooidal apertures in free-walled genera are occupied by cancelli (Fig. 8). In contrast, the calcified frontal walls of the autozooids themselves occupy these areas in fixed-walled species (Fig. 8). Regardless of whether the free- or fixed-walled organization is the more primitive (see the inconclusive discussion in Boardman *et al.*, 1992), the existence of both organizations in the demonstrably monophyletic melicerititids shows that at least one of the organizational types must be polyphyletic in cyclostomes as a whole.

Zooid structure

Melicerititids are notable among cyclostome bryozoans for their high levels of zooidal polymorphism (Taylor, 1986*a*). Polymorphism is defined as discontinuous variation in morphology between zooids within a colony, and is known or inferred to reflect differences in function between zooids (see Boardman & Cheetham, 1973). Although different polymorphs are recognized morphologically, their naming in both Recent and fossil bryozoans is usually based on presumed function rather than homology (see Silén, 1977). This can be a difficult task in fossil bryozoans. A fundamental division is made between feeding zooids, termed **autozooids**, and non-feeding zooids, termed **heterozooids**. Sometimes two autozooidal polymorphs are present, for example the A- and B-zooids of the cheilostome *Steginoporella* (Banta, 1973).



fixed-walled organization



free-walled organization

Fig. 8 Diagrammatic illustration comparing fixed-walled and free-walled organizations in melicerititid cyclostomes.

Heterozooids in modern cyclostome bryozoans include **gonozooids** (sometimes called gynozooids to avoid terminological and functional confusion with androzooids; Silén, 1977), in which larvae are brooded, and **kenozooids** which is a 'wastebasket' category of atrophied zooids seemingly having space-filling roles. Both of these heterozooid types can be distinguished with relative ease in melicerititids as they differ little from the same polymorphs in modern species of cyclostomes.

Most melicerititids have an additional group of polymorphs characterized by opercula and apertures which are modified relative to other zooids in the colony. These have been termed **eleozooids** by Taylor (1986*a*), a derivative of Canu's (1897*a*) term 'eleocellaires'.

Internal morphology

Like most stenolaemates, the proximal parts of the zooids in **endozones** are long, narrow, thin-walled tubes orientated subparallel to growth direction (Fig. 9). With growth they gradually diverge from the branch axis and enter the **exozone**. At the endozone-exozone junction, zooids rapidly increase in width, their walls thicken, and they bend to become orientated almost perpendicular to the branch surface. Differences between melicerititid polymorphs generally only become clear in the exozone and are much more apparent on the colony surface than in tangential or other sections cut through colonies.

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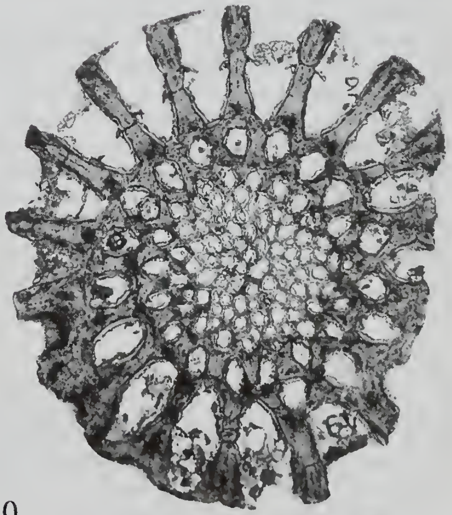

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Figs 9–10 Thin sections of a typical dendroid melicerititid, *Meliceritites palpebrosa* Levinsen, 1912; USNM 2634–16, Coniacian [?Santonian], Villedieu, Loir-et-Cher, France; 9, longitudinal section showing long, club-shaped zooids originating in the endozone, × 16; 10, transverse section showing small diameter of zooids in the endozone and spiral arrangement of buds becoming evident at the endozone-exozone transition, × 40.

Transverse sections of melicerititid branches are notable for the strong contrast between the abundance of small diameter zooidal tubes in the endozone and the fewer large zooidal tubes in the exozone (Fig. 10). Budding of zooidal tubes occurs entirely in the endozone, with the exception of some very small polymorphs (e.g. demizooids in *Atagma*) and the cancelli of *Foricula* and *Biforicula*, which may bud in the shallower parts of the exozone close to the colony surface. Sometimes the zooids are arranged in spiralling rows in the outer endozone and exozone (McKinney, 1975; Fig. 10). At the bases of erect colonies and in unilamellar and multilamellar colonies, new buds arise by division of vertical interior walls at their junction with a basal budding lamina of exterior wall. Bilamellar colonies have a similar style of budding but here the budding lamina is an interior wall (Figs 26–27). Dendroid colonies with axial canals may display budding around the periphery of the canal (McKinney, 1975: pl. 3, fig. 3a).

Intrazooidal structures are few within the endozone. Occasional thin **diaphragms** have been observed in some species (e.g. basal diaphragms in *Foricula* spp.), and **mural spines** are present deep within the endozone in zooids of *Elea triangularis* (Michelin) (Fig. 93). However, it should be noted that only a small minority of species have been studied in thin section and it is possible that internal structures are as yet undetected in other species.

Early astogeny

Early growth stages are known in very few species. While the bulk of melicerititid specimens are fragments from distal parts of colonies, those specimens which do preserve proximal parts generally have them completely obscured by the overgrowth of later zooids. Nevertheless, a few examples have been found of ancestrulae and succeeding zooids from the primary zone of astogenetic change. In all cases the **ancestrula** has a large protoecium (= primary disc) and a comparatively short distal tube (e.g. Fig. 288). This contrasts with most tubuliporine cyclostomes in which the distal tube is appreciably longer than the protoecium. Opercula have not been observed in-situ, but the straight proximal edge of the aperture strongly suggests that the ancestrula was operculate like the zooids of later astogenetic stages. The primary zone of astogenetic change shows the progressive increase in zooid size which is typical of early colony growth in bryozoans. Unfortunately, early astogeny is unknown in free-walled melicerititids and the presumed astogenetic transition between fixed- and free-walled organization has yet to be elucidated (cf. *Cinctipora elegans* as described by Boardman *et al.*, 1992).

Autozooids

The outline shape of melicerititid autozooids varies between species but most often approximates a longitudinally elongated hexagon with two longer sides parallel to the long axis of the zooid (Fig. 11). Less commonly, autozooidal outline is 'rhomboidal', the proximal and distal sides at 90° to the long axis (Fig. 11). Four-sided, roughly diamond-shaped autozooids may also occur locally within colonies, apparently as derivatives of the hexagonal pattern in which the lateral sides have been eliminated. The distal angles of hexagonal zooids are variably rounded so that they are subparallel to the distolateral edge of the aperture, which is always positioned close to the distal end of the zooid.

Fixed-walled species have flat to slightly convex **frontal walls** pierced by pseudopores (by analogy with modern fixed-walled species, pseudopores would have been cuticle-covered during life). Whereas **pseudopore** shape varies considerably in other cyclostome groups, pseudopores in melicerititids are always circular; slit-shaped, teardrop-shaped and gull-shaped are unknown in melicerititids. The density of pseudopores characteristically declines approaching the apertural hingeline.

Zooidal boundaries vary in prominence in fixed-walled species of melicerititids. Sometimes they are defined by a slightly salient wall lacking pseudopores, but in other instances pseudoporous frontal wall appears to extend uninterrupted across the boundary from one zooid to the next. Low, rounded **tubercles** may be formed from raised patches of zooidal boundary wall at the angles of the frontal walls in some species. Their location in hexagonal autozooids generally corresponds approximately to the two ends of the apertural hingeline and the distal tip of the aperture. In *Elea labyrinthica* (Michelin), a prominent tubercle is situated distally of the aperture (Fig. 61).

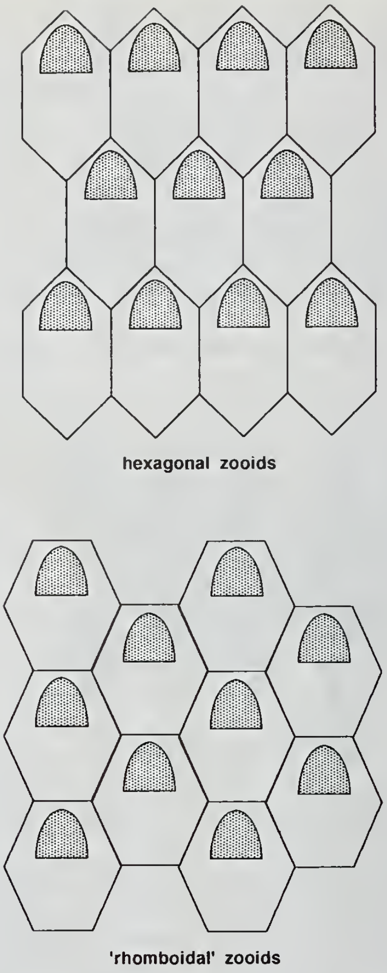


Fig. 11 Comparison between melicerititid cyclostomes with zooids of hexagonal and 'rhomboidal' surface outlines showing differences in the packing and arrangement of apertures.

Autozooid **apertures** in fixed-walled species are positioned more-or-less terminally – no or very little frontal wall is present distally of the aperture. The shape of the aperture varies between species but is relatively constant within a species and provides an extremely useful character for species recognition (Figs 14, 125). Most species have apertures which are longer than wide, some have equidimensional apertures, and a few have apertures wider than long. The proximal edge of the aperture – the hingeline – is straight or slightly convex distally (bowed). The distal edge can be well-rounded, subrounded, sub-angular, or distinctly pointed. As a result, apertural shapes found in melicerititids generally range from a semicircle at one extreme to a gothic arch at the other. More complex shapes are occasionally found, for example, the ogee-arch shaped apertures of *Reptomultelea sarissata* (Figs 282–283).

Hinge lines when well-preserved usually have a pair of small **teeth** or condyles, often with a ridge extending between them. Failure to observe these hinge teeth in some species is more likely to reflect preservational deficiency than true absence. *Meliceritites divergens* (d'Orbigny) is notable both for the large size of its hinge teeth and the presence of additional 'drop-like' teeth around the distal edge of the aperture (cf. the beading found on the distal edge of apertures in the cheilostome *Rhynchozoon*). **Apertural shelves** (e.g. Fig. 251) extend around the distal margins of the autozooidal apertures in many species of melicerititids and apparently form platform on which the closed operculum rested. Again, these vary in development between different species, ranging from barely discernable narrow shelves which are typically developed only in the distalmost parts of the aperture, to broad shelves of equal width along the entire distal margin of the aperture.

Compared with other cyclostomes, **peristomes** in melicerititids are extremely short and cannot readily be distinguished as a separate skeletal unit of the zooid. This contrasts with the long peristomes in *Plagioecia patina* and other tubuliporines which are marked by their sparse pseudopores and which may be shed as a unit during late ontogeny (see Silén & Harmelin, 1974). In the great majority of melicerititid species no more than a slightly raised apertural rim is developed. However, *Meliceritites dollfusi* Pergens has opercula located atop relatively well-defined but short peristomes.

Terminal diaphragms can be found in most melicerititid species but their distribution within colonies is generally without obvious pattern; seldom is there a clear ontogenetic zonation with terminal diaphragms in only the older, more proximal zooids, as found in many other cyclostomes (Silén & Harmelin, 1974; Boardman *et al.*, 1992). A variety of different types of terminal diaphragms can be distinguished, occasionally with more than one type being present in a single colony (or species). Some terminal diaphragms are pseudoporous (e.g. Fig. 178). These typically have a less-regular arrangement of pseudopores than is found in frontal walls. Non-pseudoporous terminal diaphragms may be planar or possess a central depression with pore (e.g. Fig. 238), reminiscent of the 'calcified terminal-vestibular membranes' known from other cyclostomes (Boardman & McKinney, 1976; Boardman *et al.*, 1992). In *Meliceritites lorieri* (Michelin) some zooids possess two or even three pores in the central depression. A third type of terminal diaphragm comprises an apparently simple, flat plate (e.g. Fig. 252). The exact location within the zooid of terminal diaphragms varies: some are positioned at about the same level as the operculum, but others are situated more proximally, occasionally beneath the apertural shelf (Fig. 252). Terminal diaphragms in relatively proximal positions may underlie in-situ opercula, as can be observed in thin sections or externally when in-situ opercula are damaged (Fig. 240). This implies that opercula do not necessarily have to be lost or shed before a terminal diaphragm can be secreted.

Calcified **opercula** (Fig. 12) are known or inferred to be a feature of all species of melicerititids. In most species they are commonly found in-situ, but in a few species in-situ opercula are extremely rare (e.g. *Meliceritites transversa* Canu & Bassler). Opercula are occasionally found very close to the growing edge of the colony, sometimes within incompletely-formed apertures. Melicerititid opercula are undoubtedly exterior walls (i.e. with cuticle-covered external surfaces during life), even in the free-walled genera *Foricula* and *Biforicula*. However, their microstructure and ultrastructure differs from that of exterior frontal walls. The outer surface of exceptionally well-preserved opercula is marked by a series of radial fissures which are orientated parallel to local growth direction (e.g. Fig. 88). Poorly-preserved opercula often have a 'recrystallized' appearance with a strong fabric in the same orientation as these fissures (e.g. Fig. 101). Pseudopores are seemingly ubiquitous in melicerititid opercula but in only a few species are they near circular in shape and approximately evenly distributed over the surface of the operculum (e.g. Fig. 214). More often they are arranged in a crescent parallel to the distolateral edge of the structure and are slit-shaped, elongated parallel to local growth direction, (e.g. Figs 69, 88, 140, 186, 254). The inner surfaces of opercula possess a pair of ridges just inward of their lateral margins (Fig. 92). These ridges, termed **sclerites** by analogy with similar thickenings found in the opercula of cheilostomes, can be observed in sections of in-situ opercula, opercula dissected out of apertures, and are also sometimes visible as moulds left in the sediment filling the zooidal chamber after loss of the operculum (Figs 176, 266). Melicerititid sclerites are generally most pronounced close to the hinge line and become reduced distally. They often slope inwards towards the median line of the operculum. When the opercular pseudopores are arranged in a crescent, they are found to open immediately inwards of the sclerites. A shallow, dimple-like depression can often be seen on the outer surfaces of well-preserved opercula in the middle of the proximal edge, i.e. adjacent to the median bar of the hingeline in articulated opercula. External surfaces of opercula tend to lack ornament, although slight patterning is found in a few species (e.g. Fig. 58).

Autozooids with an additional rim within the main aperture are common in melicerititids (Figs 34, 45, 52–53, 55, 70, 89, 177) and were called regenerations by Levinsen (1912). This phenomenon should not however be confused with polypide regeneration, the routine process of formation of a new polypide (essentially gut and tentacles) by a zooid in which the old polypide has degenerated. Instead, analogy with cheilostomes (see Banta, 1969; Taylor, 1988) suggests that the 'regenerations' of melicerititids probably resulted from the budding of a new zooid within the skeletal chamber of a dead zooid and are better termed **intramural buds**. While autozooids are often budded intramurally into the chambers of old autozooids, eleozooids can also be intramurally budded into a host autozooidal chamber (Figs 19, 57, 111, 114, 156, 165, 171, 190, 195–196). Melicerititids are outstanding among cyclostomes in their high frequencies of intramural budding; Levinsen (1912) was able to point to only a few indistinct cases of 'regenerations' in *Entalophora madreporacea* and *Hornera lichenoides* among non-melicerititid cyclostomes.

Eleozooids

Melicerititid eleozooids are the morphological analogues of cheilostome avicularia in representing zooids with modified opercula (and apertures). However, whereas avicularia invariably have hypertrophied opercula, the opercula of

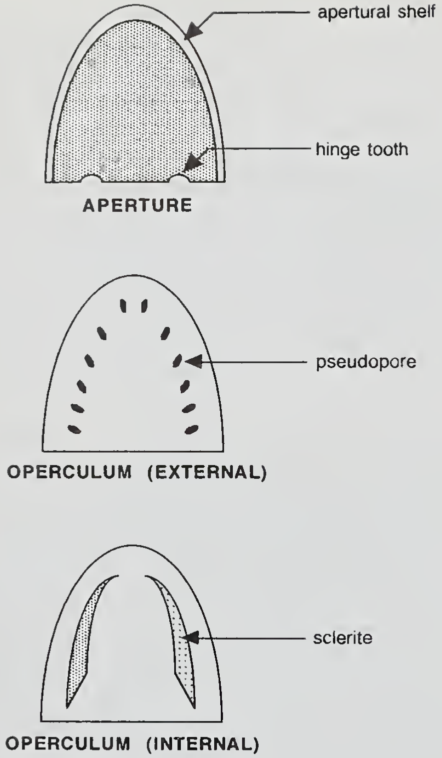


Fig. 12 Diagrammatic illustration of apertural and opercular morphology in melicerititid cyclostomes.

eleozooids may be hypertrophied or of reduced size relative to apertures of autozooids in the same colony. Eleozooids have no close analogues among modern cyclostomes but resemble the avicularia of cheilostomes. Avicularia are polymorphs with hypertrophied opercula, variously enlarged as mandibles or hair-like setae, and probably with a range of functions including defence, cleaning and even colony locomotion (see Winston, 1984, 1986, 1991). Normally, avicularia are heterozooids which are unable to feed, but occasionally they possess a feeding polypide and are therefore autozooidal polymorphs (Silén, 1977; Cook, 1979). Several different types of avicularia can be present within single colonies of some cheilostome species. Similarly, melicerititids may have several types of eleozooids within a single colony. There are frequently two types of eleozooids, one of which is larger and the other smaller than the autozooids in the colony. The restricted apertures of many eleozooids leads to the inference that they lacked a protrusible polypide, were incapable of feeding and are therefore classified as heterozooids. However, some of the larger eleozooids have apertures of sufficient size to have allowed protrusion of a polypide and it is possible that they were autozooidal polymorphs capable of feeding.

Three end-member categories of eleozooids can be recognized, termed rostrozooids, trifoliozooids and demizooids (Taylor, 1986*a*). Although most eleozooids are readily categorized into one of these types, some species possess eleozooids which are consistently difficult to classify. For example, the eleozooids of *Meliceritites magnifica* (d'Orbigny) (see Taylor, 1986*a*: fig. 2D) are rostrozooid-like in size but have trifoliate apertures, whereas the eleozooids of *Reptomultelea reussi* (Pergens) (see p. 94) have the size of demizooids or trifoliozooids but apertures resembling rostrozooids. In addition, species with two types of eleozooids occasionally possess zooids with morphologies intermediate between the two types. In all three types of eleozooids, the frontal walls of fixed-walled species have an equivalent density of pseudopores as autozooids in the same colony. In this respect eleozooids differ from gonozooids which are characterized by a high density of pseudopores.

Rostrozooids (e.g. Figs 39, 48, 63, 142–145, 180, 201, 208, 223, 255, 295) have their apertures prolonged distally into a shelf-like platform, the **rostrum**. The frontal area of a rostrozooid typically exceeds that of an autozooid in the same colony, and the rostrum may occlude a distal zooid which would otherwise have apparently developed into a normal autozooid (i.e. the rostrozooid takes the position of two autozooids on the colony surface; see Boardman in Boardman *et al.*, 1983: fig. 49.1 and 49.2). Zooids adjacent to the rostrum may be effected by its presence, sometimes developing as kenozooids (Fig. 143) and sometimes as autozooids but with obliquely-directed apertures (e.g., in *Meliceritites lorieri* the apertures of autozooids on either side of the rostrum are turned inwards towards the rostrozooid). Apertures of rostrozooids vary in morphology from almost semicircular and only slightly larger than an autozooidal aperture, to long and distally pointed, or long and distally rounded and with sides parallel or distinctly spatulate. In-situ opercula appear to be less common in rostrozooids than in autozooids, although this has not been tested quantitatively. Like autozooidal opercula, however, the opercula of rostrozooids often have a cresentic arrangement of slit-shaped pseudopores. Inner surfaces have been observed in only a few cases. Surprisingly, sclerites of the type seen in autozooidal opercula seem to be lacking in rostrozooidal opercula of *Meliceritites tuberosa* (d'Orbigny), although a marginal thickening does appear to be present. Rostrozooids are seldom arranged in regular or predictable patterns. In some species, however, rostrozooids may be clustered in groups of two or three, and they often occur in particularly high concentrations in the basal encrusting parts of erect species. Whereas frontal walls are lacking in the autozooids of the free-walled genera *Foricula* and *Biforicula*, it is notable that a small area of pseudoporous frontal wall is sometimes present in the rostrozooids. Together with the gonozooids, which are also fixed-walled in these genera, this gives colonies a mixed free-/fixed-walled organization within zones of astogenetic repetition. Intramural buds are commonly found within rostrozooids. These can be smaller rostrozooids (Figs 81, 145), trifoliozooids, demizooids or autozooids (Fig. 242). Multiple intramural rostrozooids commonly occur in some species, often with the distal ends of each successive rostrozooid being slightly elevated relative to the previous rostrozooid so that the aperture becomes inclined at a progressively greater angle to the colony surface. Two demizooids may sometimes occur as intramural buds within a single rostrozooid of *Atagma*.

Trifoliozooids (Figs 23, 164, 189) are distinguished by having apertures with a trifoliate opening in the shape of an inverted 'T'. On closer inspection of well-preserved examples, the opening is usually seen to be set within a D-shaped area which is occupied by the operculum on the few occasions that this is observed in-situ. Apertures are smaller than those of autozooids, sometimes only slightly so, however. The frontal wall of trifoliozooids bears the same density of pseudopores as an autozooid and varies from a little smaller to considerably smaller than that of an autozooid. Like rostrozooids, trifoliozooids may be concentrated in the encrusting bases of erect colonies. They may also occur with increased frequency in disrupted areas where crowding appears to have prevented the development of autozooids. Some species of *Meliceritella* have reverse (dorsal) branch surfaces composed of trifoliozooids, generally in combination with kenozooids. Trifoliozooids frequently occur as intramural buds within autozooids and sometimes within rostrozooids.

Demizooids are small eleozooids with simple D-shaped apertures and similarly shaped opercula. They show similarities to trifoliozooids in size, variation and distribution. Species of *Atagma* are particularly characterized by large numbers of demizooids which typically outnumber and may completely enclose the autozooids in the colony. Like trifoliozooids, demizooids can be found as intramural buds within both autozooids and rostrozooids.

Kenozooids

In fixed-walled melicerititids kenozooids are generally sealed by a calcified frontal wall, lack an aperture, and are identical in morphology to the kenozooids found in other tubuliporine cyclostomes. They are invariably smaller than autozooids and often more irregular in outline shape. Kenozooids are typically found in areas of growth disruption, including anastomoses (Figs. 228–229), bifurcations (Fig. 68), adjacent to gonozooids (Fig. 75) and eleozooids (Figs 143, 217), and also in the encrusting bases of erect colonies (Fig. 32). Some frontally-budded overgrowths commence with an apparent kenozooid and may include other kenozooids within the associated secondary zone of astogenetic change. Overgrowths of apparently open kenozooids, covering autozooidal frontal walls but leaving their apertures uncovered, are occasionally found in fixed-walled species (Fig. 79).

The small openings between autozooidal apertures of free-walled melicerititids were considered by Taylor (1986*a*) to be 'interzooidal spaces' rather than kenozooids because of their origin very close to the colony surface. These structures resemble the cancelli of hornerid cyclostomes and are accordingly given the same name. In neither melicerititids nor hornerids is the phylogeny of the group sufficiently well-known to determine whether the cancelli had an evolutionary origin as modified zooids or are non-zooidal in origin.

Gonozooids

Gonozooids, like those of many species of cyclostomes, are comparatively uncommon and have yet to be discovered in some melicerititid species. When known they are very similar to the gonozooids found in other tubuliporine cyclostomes, and also in articulate cyclostomes. Variation of gonozooid morphology within the melicerititids is slight. The distal frontal wall is bulbous, bears a high density of pseudopores, and in outline shape is usually longitudinally elliptical (e.g. Figs 24–25, 41, 65, 71, 78, 86, 262), occasionally more equidimensional (Fig. 236), and sometimes rounded-subtriangular with an almost straight distal edge (Fig. 209). Seldom do the neighbouring autozooids significantly indent the outline of the distal frontal wall (cf. Fig. 209), and they have never been found to pierce the frontal wall (cf. tubuliporines such as *Plagioecia*). Asymmetrical distal frontal walls are occasionally found in which the axis of the gonozooid bends significantly from local colony growth direction and the ooeciopore opens laterally or obliquely.

The proximal end of the gonozooid appear identical to an autozooid – in fixed-walled species, it has a typically hexagonal frontal wall with the same density of pseudopores as an autozooid and a D-shaped opening similar to an autozooidal aperture. However, instead of being closed by an operculum, the D-shaped opening ('maternal aperture') forms the point of origin of the densely-pseudoporous distal frontal wall of the gonozooid (Fig. 42). Sometimes the distal frontal wall is initially a parallel-sided tube before dilation (Fig. 35), and in a few species (e.g. *Meliceritites dollfusi* Pergens) it grows proximally to cover the autozooid-like proximal frontal wall.

The ooeciopore is situated terminally and is usually transversely elliptical (Figs 138, 153, 166, 222, 292), less often subcircular (Fig. 65). Transverse width tends to be roughly the same as that of autozooids in the same colony. Rarely, the distal rim is prolonged into a slight tongue overhanging the ooeciopore. Significant ooeciostomes are lacking, even in well-preserved material where breakage can be ruled out. Teratological specimens include partially-formed, aborted gonozooids (Fig. 43), and coalesced gonozooids sharing a single ooeciopore (Fig. 147)

In all melicerititids with suitably broken gonozooids, a low ring diaphragm occurs in the distal part of the gonozooid just proximal to the ooeciopore (Figs 25, 71). This structure was first observed by Levinsen (1912) who termed it the **atrial ring** and noted the presence of a similar structure in the articulate cyclostome *Crisia eburnea* (Levinsen, 1912: pl. 7, fig. 12).

Removal of the roof allows the floor of the gonozooid to be examined. Traces of zooids which failed to reach the colony surface are visible through the basal wall of the gonozooid (e.g. Figs 24–25). The floor of the gonozooid may consist of a series of walls occluding the underlying zooids (e.g. Taylor, 1986*a*: fig. 3B). These overgrown zooids usually lack frontal walls, but in some cases possess a frontal wall and fully-formed D-shaped aperture (e.g. Levinsen, 1912: pl. 7, fig. 13), a condition found especially in zooids located more proximally beneath the dilated part of the gonozooid. Such features seem to indicate that development of the dilated part of the gonozooid was often retarded relative to the development of nearby autozooids.

Intramural buds have never been seen within gonozooids, nor have gonozooids been observed to originate as intramural buds.

STRATIGRAPHICAL DISTRIBUTION

The 36 species of fixed-walled lamellar melicerititids described here range from Albian to Campanian in age. Although species belonging to other melicerititid genera occur in the Barremian, Aptian, Maastrichtian and Palaeocene, there are no known species of *Elea*, *Semielea* or *Reptomultelea* in deposits of these ages. The peak diversity for lamellar melicerititid species occurs in the Cenomanian, which contains 17 species. Diversities of 7–9 species characterize the Turonian, Coniacian and Santonian, whereas the Albian and Campanian contain only 3 and 2 species respectively. This diversity pattern can be contrasted with the pattern for melicerititid species as a whole (Taylor 1986*a*, fig.

4; nb. constructed from a less complete database), which shows a Santonian peak in diversity. The anomolously large number of lamellar species in the Cenomanian probably correlates with the greater availability of nearshore localities, where species of *Reptomultelea* are particularly common.

Stratigraphical ranges of species of *Elea* and *Reptomultelea* are given in Figures 16 and 127 respectively. Most species are recorded from one stratigraphical stage only, but a few range through two or three stages. Better sampling will inevitably extend these ranges and caution should therefore be exercised when using melicerititids as age indicators.

SYSTEMATIC PALAEONTOLOGY

Specimen repositories and abbreviations. Specimens studied are housed in the following collections: BGS, British Geological Survey, Keyworth; BMNH, The Natural History Museum, London; DM, Dresden Museum (Reuss Collection); EM, Essener Museum; MNHN, Muséum National d'Histoire Naturelle, Paris; PSUB, Goldfuss Collection, Universität Bonn; SMD, Staatl. Museum Mineralogie und Geologie, Dresden; USNM, National Museum of Natural History, Smithsonian Institution, Washington; VH, Voigt Collection, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg; ZMC, Zoologisk Museum, Copenhagen.

Methods of study. Almost all of the species described have been studied primarily using scanning electron microscopy (SEM), and whenever possible type specimens have been scanned. Application of SEM is becoming increasingly essential in bryozoology, both for the precise characterization of species and for their clear photographic illustration (Taylor, 1990). In the case of *Semielea dichotoma*, however, no material was available for SEM. Most SEM has been undertaken on uncoated specimens in an environmental chamber (Taylor, 1986*b*), using either ISI 60-A or ISI ABT-55 scanning electron microscopes. Unless otherwise stated, all of the scanning electron micrographs depicted here are images formed by back-scattered electrons (cf. secondary electron images which are more conventional in SEM of coated specimens, e.g. Fig. 180). It must be emphasized that the magnifications of these figures are very approximate because of highly imprecise machine readings.

Morphometrical determinations have been made using an eyepiece micrometer affixed to a Wild M7 binocular microscope. Time limitations have meant that for most species autozooidal dimensions have been determined from a single specimen only, preferably the holotype or lectotype. Intracolony variability within a species is therefore poorly known and deserves future study. Ten autozooids per colony have been measured in most species. Mean, standard deviation (SD), coefficient of variation (CV) and observed range are given. For eleozooids and gonozooids it has often been necessary to take measurements from several colonies to obtain a reasonable sample size. Figure 13 summarizes the principal measurements made on autozooids (and eleozooids); see Pitt & Taylor (1990: fig. 2) for comparable measurements made on gonozooids. When present in sufficient numbers, apertural measurements were made from zooids with in-situ opercula, as these have clearly-defined edges.

Orientated thin sections (longitudinal, tangential and transverse) were prepared for a small number of species using a similar method to that described by Nye *et al.* (1972).

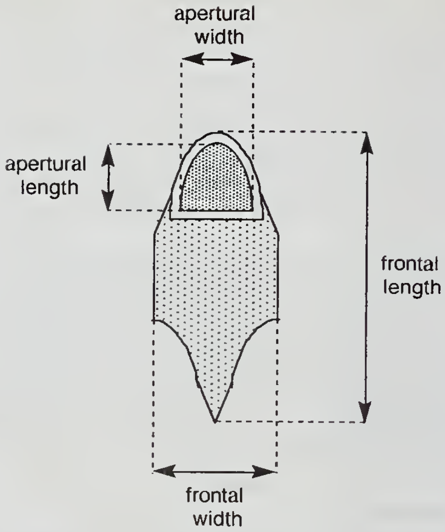


Fig. 13 Measured zooidal dimensions.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **ELEIDAE** d'Orbigny, 1852

REVISED DIAGNOSIS. Colony erect, dendroid, tubular, bifoliate or fenestrate; or encrusting, multiserial and generally multilamellar; overgrowths originating by intrazooecial fission and eruptive budding onto the colony surface, initiating a secondary zone of astogenetic change. Skeletal organization fixed-walled or free-walled, in some species varying according to polymorph type. Interior wall microstructure tripartite, apparently with a layer of transverse fibres flanked by lamellar layers. Ancestrula with a short distal tube. Zooidal polymorphism well-developed, most species possessing one or more types of eleozooids in addition to the autozooids, gonozooids and kenozooids. Autozooids fixed- or free-walled, operculate; operculum calcified, articulated with the straight proximal hingeline of the aperture, semicircular or arch-like in outline shape and bearing sclerites on the inner surface; peristome lacking. Eleozooids fixed- or free-walled, with opercula elongated to form pointed, rounded or spatulate mandibles in rostrozooids, reduced relative to autozooidal opercula in the smaller trifoliozooids and demizooids. Gonozooids non-operculate, fixed-walled with distal frontal walls densely pseudoporous and longitudinally elliptical (occasionally subtriangular) in outline shape, neither penetrated nor significantly indented by autozooids; ooeciopore terminal, transversely elliptical to subcircular; ooeciostome short; ring diaphragm (atrial ring) of low relief present just proximal to ooeciopore. Intramural budding common, often involving budding of a different polymorph type within the skeletal chamber of a host zooid.

REMARKS. The Family Eleidae d'Orbigny, 1852 antedates Melicerititidae Pergens, 1890 and, although priority is not mandatory with regard to family names, Eleidae is here preferred but the term 'melicerititid' is retained for vernacular purposes.

Melicerititids have a clear autapomorphy in the possession of a calcified operculum, hinged to the proximal edge of the aperture and able to seal the zooid on closure. No other cyclostomes are known to have calcified (or uncalcified) opercula. The high level of polymorphism in melicerititids undoubtedly relates to the presence of this operculum which can be modified to form various polymorphs, analagous to the avicularia of cheilostomes derived by differentiation of the operculum (Taylor, 1986*a*).

Eight genera of melicerititids are recognized (Table 2). These are distinguished principally according to the traditional character of colony-form. A full phylogenetic analysis of the group will be necessary to determine whether zooid-level characters may be significant in an improved generic subdivision.

DISTRIBUTION. Barremian-Danian (or Montian), Europe and western Asia.

Genus *ELEA* d'Orbigny, 1853

TYPE SPECIES. *Bidiastopora lamellosa* d'Orbigny, 1850, designated by Gregory (1899, p. 299).

OTHER SPECIES. *Elea elegantula* sp. nov., *Elea flabellata* sp. nov., *Elea hexagona* d'Orbigny, 1853, *Eschara labyrinthica* Michelin, 1843, *Elea mackinneyi* sp. nov., *Elea pseudolamellosa* sp. nov., *Elea subhexagona* sp. nov., *Eschara triangularis* Michelin, 1841, *Elea viskovae* sp. nov., *Elea whiteleyi* sp. nov.

REVISED DIAGNOSIS. Eleid with bifoliate colony-form; autozooids with a fixed-walled organization; cancelli lacking.

REMARKS. D'Orbigny's (1853) original description of this genus emphasized its similarities to *Meliceritites* from which it was distinguished by the bifoliate form of the colony. Without choosing a type species, d'Orbigny included the following ten species in his new genus: *Diastopora cervicornis* Michelin, 1845, *Bidiastopora ramossisima* d'Orbigny, 1850, *Eschara ranvilliana* Michelin, 1845, *Elea calloviensis* sp. nov., *Elea reticulata* sp. nov., *Eschara triangularis* Michelin, 1841, *Elea rhomboidalis* sp. nov., *Elea turoniensis* sp. nov., *Elea lamellosa* sp. nov., and *Elea hexagona* sp. nov. The first four species are from the Jurassic and are not melicerititids; all four were placed in synonymy with *Multisparsa lamellosa* (Michelin, 1845) by Walter (1970). *Elea reticulata* from the Neocomian is also not a melicerititid. Walter (1985) assigned it to the tubuliporine genus *Mesenteripora*, as *Mesenteripora reticulata* (d'Orbigny, 1853). *E. turoniensis*, from the Turonian of Sainte-Maure (Indre-et-Loire), is represented by four specimens registered as No. 6964 in the d'Orbigny Collection, MNHN, including one specimen in a glass tube here designated as the lectotype (Voigt photocard 6959). This too is not a melicerititid. The remaining species listed by d'Orbigny are true melicerititids and are correctly assigned to the Family Eleidae.

Table 2 Key to melicerititid genera.

1.	Organization fixed-walled (i.e. autozooids with pseudoporous frontal walls; cancelli lacking)	2
	Organization free-walled (i.e. autozooids lacking pseudoporous frontal walls; cancelli present)	7
2.	Colony entirely encrusting	*Reptomultelea*
	Colony erect	3
3.	Branches bilaminate, strap-like or frondose	*Elea*
	Branches dendroid, circular or subcircular in cross-section	4
4.	Branches hollow	*Semielea*
	Branches solid	5
5.	Autozooids absent on one side of branch	*Meliceritella*
	Autozooids present around entire circumference of branch	6
6.	Autozooids surrounded by numerous small eleozooids with D-shaped apertures	*Atagma*
	Otherwise	*Meliceritites*
7.	Branches bilaminate, strap-like or frondose	*Biforicula*
	Branches dendroid, circular or subcircular in cross-section	*Foricula*

Elea meridiana, described by Lang (in Woods, 1906: p. 283) from the Cretaceous [?Campanian] of Pondoland, South Africa is a bifoliate tubuliporine, not a melicerititid. Three figured syntype fragments are registered in the BMNH collections as D11834.

Among the eleven species validly assigned to *Elea*, a few subgroupings may be recognized. One subgrouping comprises *Elea elegantula* sp. nov. from the Lower Cenomanian, *E. subhexagona* sp. nov. from the Upper Cenomanian and Turonian, and *E. hexagona* d'Orbigny from the Santonian, three species with adeoniform colonies and very similar zooidal morphologies. They can be reasonably interpreted as members of a clade exhibiting an evolutionary trend towards an increase in the size of the autozooidal aperture relative to the frontal wall. *E. lamellosa* (d'Orbigny) and *E. pseudolamellosa* sp. nov. can be distinguished only by the morphology of the eleozooidal apertures which have an inverted T-shape in the former (trifoliozooid-type) but are D-shaped in the latter (demizooid-type). Other species of *Elea* (e.g. *E. triangularis* (Michelin) and *E. whiteleyi* sp. nov.) are very distinctive and more difficult to relate to congeneric species. *E. whiteleyi* from the Lower-Middle Cenomanian may be a member of the stem-group of *Biforicula*, judging by the similarity of its small eleozooids to those of the earliest species of *Biforicula*, *B. multicincta* from the Upper Cenomanian (see Voigt 1989). Table 3 is a key to the identification of species of *Elea* and should be used in conjunction with Figures 14 and 15, which show the characteristic outline shapes of the autozooidal and eleozooidal apertures respectively.

It is worthwhile speculating on the phylogenetic origin of *Elea*. Assuming that the genus originated from a fixed-walled ancestor, there are two main possible ancestral genera: *Meliceritites* and *Reptomultelea*. Origination from *Meliceritites* would require a change in the mode of erect growth from dendroid to bifoliate, whereas origination from *Reptomultelea* would require the acquisition of erect growth. The latter hypothesis is favoured for two reasons: (1) extensive *Reptomultelea*-like bases are often present in species of *Elea*, and (2) similarities exist between species of *Elea* and *Reptomultelea* in the shape of the acuminate eleozooids (rostrozooids). Full phylogenetic analysis is, however, needed. Stratigraphical distribution is not helpful in this respect as *Reptomultelea* and *Elea* both have their earliest known occurrences in the Lower Albian while *Meliceritites* ranges back to the Upper Barremian.

DISTRIBUTION. Lower Albian-Upper Campanian (Fig. 16) of France, Germany, England and Kazakhstan.

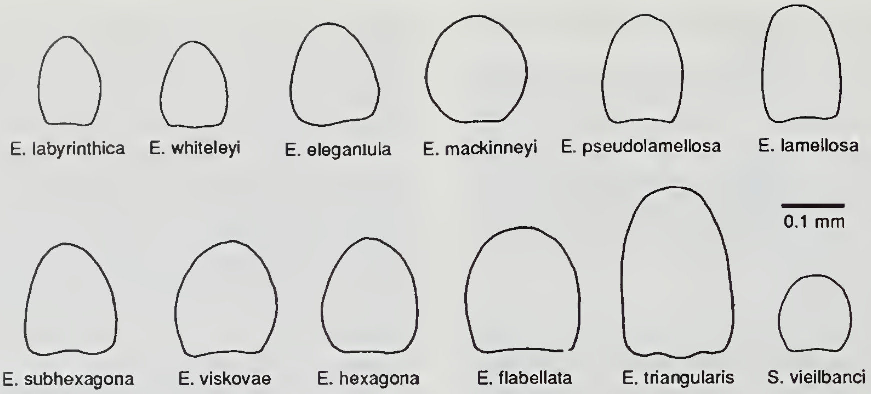


Fig. 14 Outlines of autozooidal aperture shapes in species of *Elea* and *Semielea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

Elea lamellosa (d'Orbigny, 1850) Figs 17–28

1850 *Bidiastopora lamellosa* d'Orbigny: 266.
1851 *Bidiastopora lamellosa* d'Orbigny; d'Orbigny, pl. 625, figs 11–15.
1853 *Elea lamellosa* (d'Orbigny); d'Orbigny: 632.
1853 *Semielea plana* d'Orbigny: 638, pl. 738, figs 12–14.
?1853 *Reptelea pulchella* d'Orbigny: 642, pl. 738, figs 16–17.
1853 *Semimultelea irregularis* d'Orbigny: 652, pl. 741, figs 6–8.
1853 *Semimultelea gradata* d'Orbigny: 653 (partim), ?non pl. 741, figs 9–13.
1890 *Semielea plana* d'Orbigny; Pergens: 393.
1890 *Elea lamellosa* (d'Orbigny); Pergens: 398.
1899 *Reptelea pulchella* d'Orbigny; Gregory: 292, non fig. 31.
1899 *Elea lamellosa* (d'Orbigny); Gregory: 299.
non 1899 *Semimultelea irregularis* d'Orbigny; Gregory: 296, fig. 32.
1912 *Meliceritites plana* (d'Orbigny); Levinsen: 43, pl. 5, figs 11–12.
1912 *Meliceritites lamellosa* (d'Orbigny); Levinsen: 45, pl. 3, figs 1–9.
1985*a* *Elea lamellosa* (d'Orbigny); Taylor, fig. 2F and G.
1985*b* *Semielea plana* d'Orbigny; Voigt: 631, pl. 3, figs 16–17.

MATERIAL. Type: no type specimens have been designated; the d'Orbigny Collection, MNHN includes 8 glass tubes, all registered as 8191, each of which contains specimens of *Elea lamellosa* (e.g.Fig. 17). Some of these are from the two localities given in the original species description (i.e. Tours and Saintes); a lectotype could be selected from among these topotypic syntypes but the identity of the species is not in doubt.

Other material: MNHN d'Orbigny Colln 8191 (Voigt photocard 8310), Senonian [Santonian], Vendôme, France. MNHN d'Orbigny Colln 8195, specimen labelled by E. Voigt as the type of *Semielea plana* d'Orbigny (Voigt photocard 8319; figd by Voigt, 1985*b*: pl. 3, fig. 17), herein designated the lectotype of *S. plana*, Senonian, ?Tours, France. MNHN 8201 d'Orbigny Colln, specimen labelled by E. Voigt as the type of *Semimultelea irregularis* d'Orbigny (Voigt photocard 5733; figd by d'Orbigny, 1853: pl. 741, figs 6–8), herein designated the lectotype of *S. irregularis*, Senonian, Tours, France. BMNH D11786, Turonian, Touvent, Charente Inferieure, Jukes Browne Colln; D54296, Coniacian, Tours, Indre-et-Loire, Voigt Colln; D59166-7, Coniacian, Craie de Villedieu, Rue St Barthelemy, Tours, Taylor and Hammond Colln; D36195, Coniacian, St Paterne, Indre-et-Loire, Pergens Colln; D36176, Senonian, St Antoine-du-Rocher, Indre-et-Loire, Pergens Colln; D36060-2, Senonian, Vendôme, Loir-et-Cher, Pergens Colln; D53637, D59159, Coniacian or Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, Gale Colln; D59165, Coniacian or Santonian, Craie de Villedieu, Chateau Mbr, between Villedieu and Trehet on D80, Taylor and Hammond Colln; D58849 (sample), Santonian, Craie de Villedieu, Chateau Mbr, Bed 17 of Jarvis *et al.* (1982), Nowicki Colln; D58843 (sample), D59160-2, D59163 (sample), D59164, D59202-3, Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 20 of Jarvis *et al.* (1982), Villedieu, Gale Colln; D58839 (sample), Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 22a of Jarvis *et al.* (1982), Villedieu;

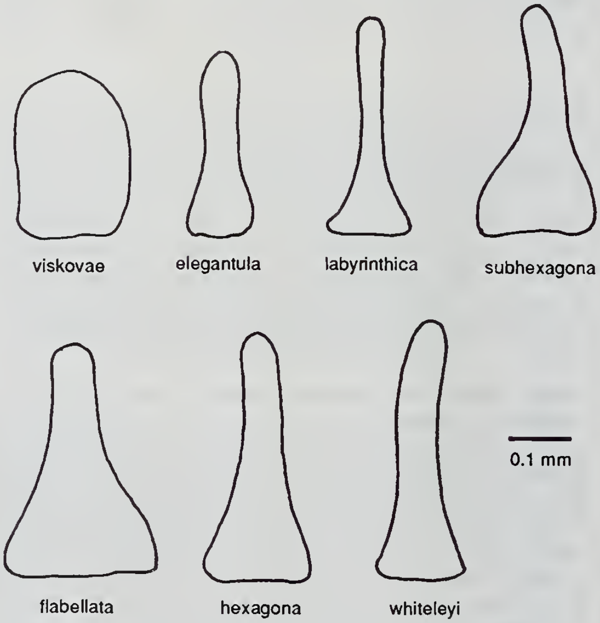


Fig. 15 Outlines of eleozooidal aperture shapes in species of *Elea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

D59168 (sample), Santonian, Craie de Blois, Rue St Barthelemy, Tours, Taylor and Hammond Colln; D59169-72, Santonian, Craie de Saintes Fm., Voiville Mbr, les Arcivaux-Portublé, Saintes, France. USNM 2737–1 to 4, Coniacian, Villedieu (sections including duplicate acetate peels in BMNH). ZMC M40, [?Coniacian or Santonian], St Antoine du Rocher, France. ZMC Levinsen material unnumbered, Coniacian, Villedieu, Canu Colln.

Un-numbered VH material from the following localities: Coniacian, Tours; Coniacian, Villedieu; Coniacian, St Christophe, Indre-et-Loire; Santonian, Vendôme; Santonian, Merpins, Charente-Maritime; Coniacian, Joué-les-Tours, Indre-et-Loire (labelled *Semimultelea irregularis*).

DESCRIPTION. Colony normally bifoliate, foliaceous (Fig. 17), with broad, folded fronds (Fig. 18), about 0·6–0·8 mm deep, anastomosing and giving rise to daughter fronds perpendicular to their surfaces; overall shapes of complete colonies are flattened spheroids, up to at least 40 mm in diameter (e.g. BMNH D59159); parts of some colonies, including extensive colony bases, are unilamellar with a concentrically ridged exterior wall forming the basal side. Growing edges revealing several generations of buds, often occluded by a combination of small eleozooids and kenozooids. Overgrowths common, formed by eruptive budding onto

Table 3 Key to the species of *Elea*. Note that because this key places a high reliance on eleozooids, which may not be developed in every specimen, identifications should be carefully checked against the full descriptions; furthermore, it is possible that new material will reveal the presence of eleozooids in species in which they are currently unknown.

1. Autozooidal aperture more than 0·25 mm long, bell-shaped; eleozooids unknown .... *Elea triangularis* (p.34)
   Autozooidal aperture less than 0·25 mm long 2
2. Eleozooids with long rostra (rostrozooids) present 3
   Rostrozooids lacking 10
3. Small eleozooids with D-shaped apertures (demizooids) abundant .... *Elea whiteleyi* (p.39)
   Demizooids lacking 4
4. A single large and prominent barkhan dune-shaped tubercle situated distally of the zooidal apertures ..... *Elea labyrinthica* (p.25)
   Otherwise 5
5. Reduced frontal wall occupying less than half of the autozooidal frontal surface; tuberculate zooidal boundaries .... *Elea flabellata* (p.20)
   Otherwise 6
6. Eleozooids with broad, well-rounded rostra 7
   Eleozooids with narrow, pointed rostra 8
7. Autozooids with broad apertural shelves; rostrozooid apertures less than 1·5 × longer than wide .... *Elea viskovae* (p.38)
   Autozooids with apertural shelf lacking or very narrow; rostrozooid apertures about twice as long as wide .... *Elea mackinneyi* (p.29)
8. Autozooids with a tubercle distal of the aperture .... *Elea hexagona* (p.23)
   Tubercle lacking 9
9. Autozooid frontal width less than 0·25 mm .... *Elea elegantula* (p.19)
   Autozooid frontal width more than 0·25 mm .... *Elea subhexagona* (p.32)
10. Eleozooids with inverted T-shaped apertures (trifoliozooids) .... *Elea lamellosa* (p.14)
    Eleozooids with D-shaped apertures (demizooids) .... *Elea pseudolamellosa* (p.30)

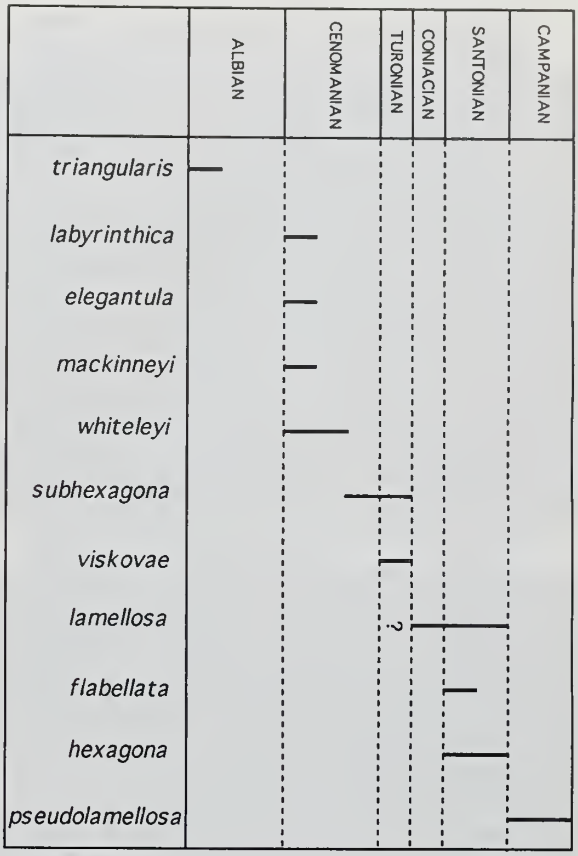
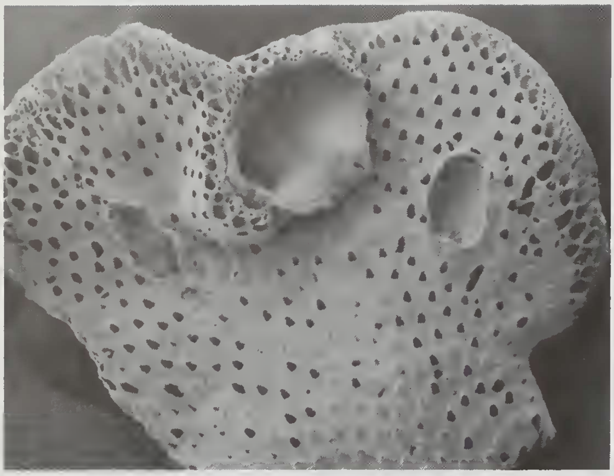


Fig. 16 Stratigraphical ranges of species of *Elea*.

Fig. 17 *Elea lamellosa* (d'Orbigny, 1850), MNHN d'Orbigny Collection 8191 (Voigt photocard 8310), Senonian [Santonian], Vendôme, France; photograph of frond fragment, × 4·8.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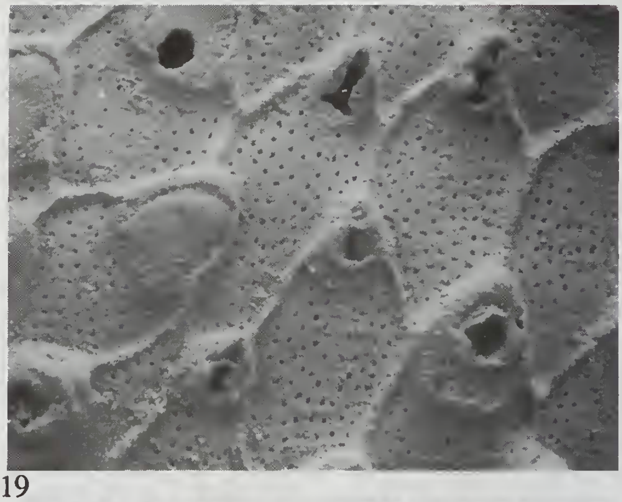
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the surface of a frond, initiating a zone of secondary astogenetic change, becoming subcircular in outline; pseudoancestrula an autozooid; autozooids in zone of change in old overgrowths often with intramurally budded eleozooids. Zooids generally arranged in quincunx; organization fixed-walled.

Autozooids (Fig. 20) medium-sized, frontally hexagonal or diamond-shaped, about 1·5 x longer than wide, outline extended distally and rounded by apertural rim; frontal wall flat or very slightly convex, with circular pseudopores; zooecial boundaries distinct, raised. Apertures (Fig. 22) small, longitudinally elongate, 1·1–1·4 x longer than wide, attaining maximum width at or a little distally of the hinge line, well-rounded distally; apertural shelf narrow; apertural rim prominent, moderately broad, continuous with raised wall forming remainder of zooecial boundary; hinge line with median bar. Opercula (Fig. 21) very often preserved in-situ, prominent, surface convex, pseudopores not observed. Terminal diaphragms not observed. Intramural eleozooids (Fig. 19) common, their inverted T-shaped apertures slightly smaller than those of primary eleozooids and occupying the distal half of the host autozooid aperture, a slightly concave pseudoporous exterior wall fills the proximal part of the host autozooid aperture.

Eleozooids abundant, distributed widely across fronds, sometimes clustered in small groups (Fig. 19), frontally 1·5–2 × longer than wide, typically a little narrower and more pointed distally than autozooids but of about the same length; frontal wall with circular pseudopores in the same density as those of the autozooids. Aperture (Fig. 23) small, longitudinally elongate, about 1·5–2 × longer than wide, attaining maximum width at the hinge line, inverted T-shaped in outline through indentation of lateral margins by the rostral shelf. Opercula rarely preserved in-situ, longitudinally elongate, rounded distally. Intramurally budded eleozooids within host eleozooids not observed.

Kenozooids often present in association with eleozooids, generally with a smaller frontal area than other zooidal polymorphs.

Gonozooids (Figs 24–25) common, sometimes paired, large, longitudinally elongate; frontal wall with a short parallel-sided portion emerging from the maternal zooidal aperture, dilating into an ovoidal bulbous portion almost twice as long as wide. Ooeciopore (Fig. 24) transversely elongate, 2–2·5 × wider than long, in outline often kidney-shaped due to the presence of an indenting proximal hemiseptum. Atrial ring (Fig. 25) well-developed.

Thin sections show median budding lamina (Figs 26–27) straight to slightly sinuous, similar to the normal interzooidal walls in microstructure; zooecia up to at least 0·63 mm in total length; frontal walls thinning distally towards hinge line; opercula (Fig. 28) thin, often less than 0·015 mm in thickness, sclerites present; interzooidal walls about 0·015 mm thick near centre of branch, increasing to 0·03–0·05 mm near surface; basal diaphragms occasionally present in proximal parts of zooids.

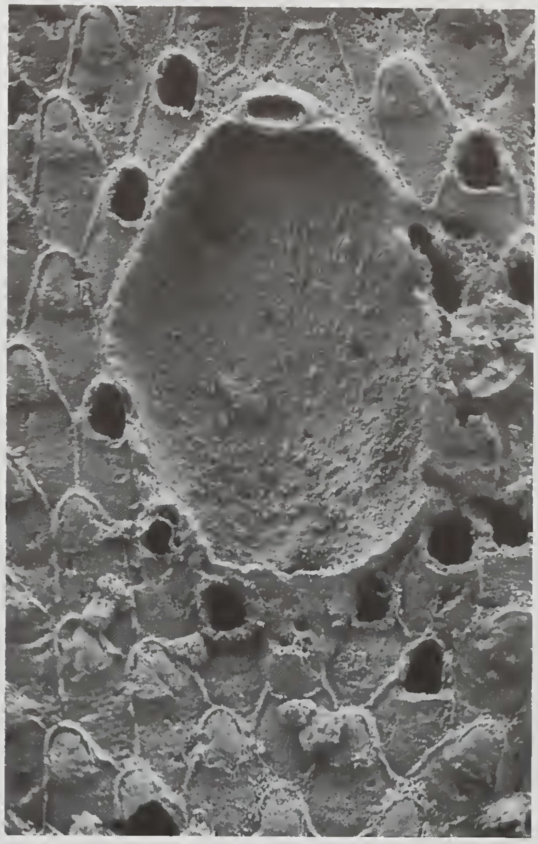


Fig. 24 *Elea lamellosa* (d'Orbigny, 1850), BMNH D59203, Santonian, Craie de Villedieu, Bouchardière Member, Villedieu, France; de-roofed gonozooid with intact ooeciopore, × 45.

Measurements.
autozooids (10 zooids with in-situ opercula from BMNH D59164)
frontal length: mean = 0·49 mm; SD = 0·040 mm; CV = 8·2; range = 0·45–0·57 mm
frontal width: mean = 0·32 mm; SD = 0·015 mm; CV = 4·9; range = 0·30–0·35 mm
apertural length: mean = 0·19 mm; SD = 0·008 mm; CV = 4·2; range = 0·18–0·20 mm
apertural width: mean = 0·16 mm; SD = 0·013 mm; CV = 8·1; range = 0·14–0·18 mm

eleozooids (10 zooids from BMNH D59164)
frontal length: mean = 0·50 mm; SD = 0·054 mm; CV = 10·9; range = 0·42–0·59 mm
frontal width: mean = 0·28 mm; SD = 0·046 mm; CV = 16·7; range = 0·18–0·33 mm
apertural length: mean = 0·10 mm; SD = 0·008 mm; CV = 8·1; range = 0·09–0·11 mm

Figs 18–23 *Elea lamellosa* (d'Orbigny, 1850). 18, BMNH D53637, Coniacian or Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, France, frond fragment with two broken gonozooids and a partly enveloped, fouling oyster, × 7·5. 19, BMNH D59164, Santonian, Craie de Villedieu, Bouchardière Mbr, Villedieu, primary eleozooids, operculate autozooids and a damaged intramural eleozooid (lower right), × 75. 20–21, ZMC Levinsen Collection M40, [?Coniacian or Santonian], St Antoine du Rocher, France; 20, regularly-arranged, operculate autozooids, × 74; 21, autozooidal operculum, × 220. 22–23, Santonian, Craie de Villedieu, Bouchardière Member, Villedieu; 22, BMNH D59203, autozooidal aperture, × 285; 23, BMNH D59202, eleozooid aperture, × 330.

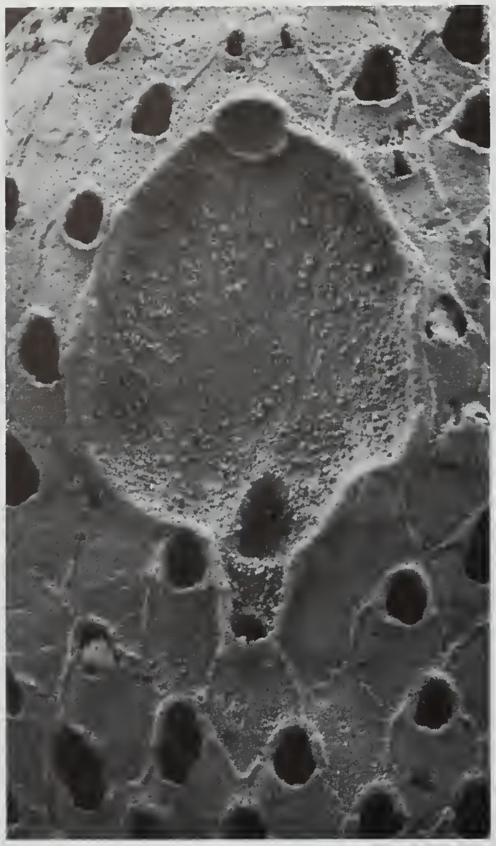
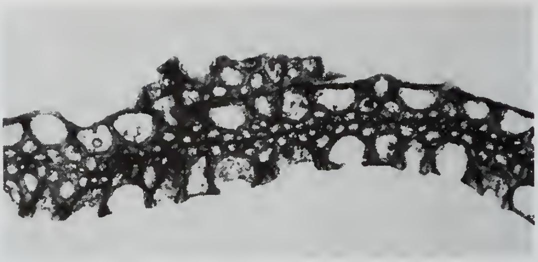


Fig. 25 *Elea lamellosa* (d'Orbigny, 1850), BMNH D59202, Santonian, Craie de Villedieu, Bouchardiére Member Villedieu, France; de-roofed gonozooid exposing entrance to maternal zooid and atrial ring, × 45.

apertural width: mean = 0·06 mm; SD = 0·009 mm; CV = 16·6; range = 0·05–0·08 mm

gonozooids (6 zooids from sample BMNH D59163)
total frontal length: range = 2·22–2·63 mm
distal frontal wall length: range = 1·86–2·25 mm
frontal width: range = 1·10–1·31 mm
ooeciopore length: range = 0·08–0·11 mm
ooeciopore width: range = 0·17–0·20 mm

REMARKS. *Elea lamellosa* is an extremely abundant bryozoan in the Coniacian-Santonian calcarenites of the Loire region, notably the Craie de Villedieu, and in approximately contemporaneous deposits in the Aquitaine Basin, for example at Saintes. It is the only bifoliate melicerititid to occur commonly in these beds, in which dendroid forms such as *Meliceritites magnifica*, *M. ornata* and *M. tuberosa* tend to dominate (Fig. 3). The foliaceous shape ('eschariform') of the colonies contrasts with most other bifoliate melicerititids which have strap-like branches ('adeoniform'). Although present in several species of *Meliceritites* and also in *Semielea vieilbanci*, no other species of *Elea* possess small eleozooids with inverted T-shaped apertures. These trifoliozooids are the principal means of distinguishing between *E. lamellosa* and the closely similar but stratigraphically younger *E. pseudolamellosa* (p. 30).



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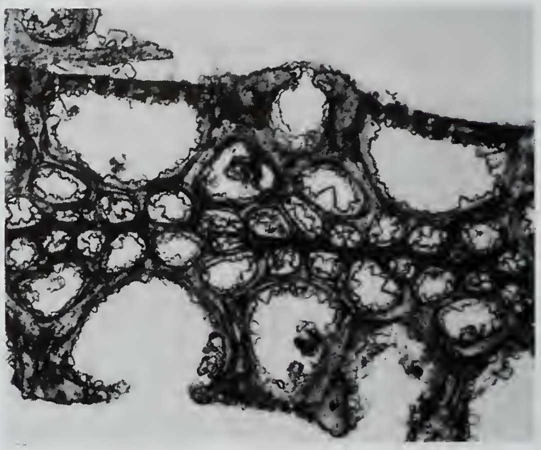

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Figs 26–28 *Elea lamellosa* (d'Orbigny, 1850), photomicrographs of thin sections of specimens from the Coniacian [?Santonian] of Villedieu, Loir-et-Cher, France. 26–27, USNM 2737–2; 26, transverse section, × 26; 27, detail showing median budding lamina and eleozooid (top centre), × 100. 28, USNM 2737–1, longitudinal section of an autozooid with in-situ operculum, × 97.

Semielea plana d'Orbigny (see Voigt, 1985*b*: pl. 3, fig. 17) is a unilamellar fragment of *Elea lamellosa* with the beginnings of an eruptive overgrowth, and *Semimultelea irregularis* d'Orbigny is the multilamellar base of an *Elea lamellosa* colony. The identity of *Reptelea pulchella* is uncertain. The lectotype (herein designated) of *R. pulchella* is MNHN d'Orbigny Collection 8196, the specimen in a tube labelled by E. Voigt as the type (Voigt photocard 8316). This Senonian specimen consists of a small colony encrusting a bivalve shell fragment. Eleozooids are lacking. It may be a young stage of *E. lamellosa* or perhaps the base of another melicerititid species.

Semimultelea gradata d'Orbigny is represented by two specimens registered as 8202 in the d'Orbigny Collection, MNHN. One of the specimens is from Tours and appears to be the basal part of a colony of *Elea lamellosa*. The second specimen, from Meudon (Campanian), labelled by E. Voigt as the type (Voigt photocard 5747), is herein designated as the lectotype. This is probably the base of an indeterminate erect melicerititid, and is unlikely to be *Elea lamellosa* in view of the otherwise absence of this species in the chalky facies of Meudon.

Semimultelea irregularis d'Orbigny was selected as the type species of *Semimultelea* d'Orbigny by Gregory (1899: p. 296). Unfortunately, Gregory's material of supposed *S. irregularis* is a mixture of indeterminate Turonian melicerititids with overgrowths, none of them conspecific with true *S. irregularis* (= *Elea lamellosa*). Nevertheless, the type species selection should stand, making the genus *Semimultelea* an objective junior synonym of *Elea*.

DISTRIBUTION. ?Turonian, Coniacian-Santonian of the Loire region and Aquitaine, France. The Turonian record is based on an old specimen (BMNH D11786) and, especially in view of correlation problems, should be regarded as doubtful.

Elea elegantula sp. nov. Figs 29–43

1985*a* *Elea* sp. Taylor, fig. 2H and I.

MATERIAL. Holotype: VH 10451, Lower Cenomanian, Mülheim/Ruhr, Germany. Paratypes: VH 9847–8, 10452, 10473, same horizon and locality as paratype. Other material: numerous un-numbered VH topotype specimens.

NAME. With reference to its elegant appearance.

DESCRIPTION. Colony bifoliate with apparently short branches, generally narrow basally and expanded distally, ranging from about 0·7–4 mm in width but typically about 1·6 mm wide, and approximately 0·4 mm deep, often divided distally and frequently twisted. Zooid arrangement varies from regular quincunx to poorly-defined transverse rows, zooids close to the branch margin slightly divergent; organization of all polymorphs fixed-walled. Overgrowths (Fig. 33) may arise through eruptive budding onto branch surface; pseudoancestrula operculate, frontal wall negligable; zone of secondary astogenetic change characterized by autozooids with smaller and more rounded apertures than those in zones of astogenetic repetition. Colony base (Figs 37–38) extensive, giving rise to multiple erect branches whose budding laminae are orientated parallel to local orientation of basal zooids. Ancestrula not observed.

Autozooids (Fig. 29) of moderate size, with pseudoporous frontal walls occupying half or more of the frontal area, about 2 × longer than wide, generally elongate hexagonal in shape with rounded distal borders; zooecial boundaries raised and well-defined. Apertures (Fig. 30) small, longitudinally elongate, up to 1·3 × longer than wide, attaining maximum width a little distal of the hinge line, rounded distally; apertural shelf well-developed, broadening distally; hinge line with a median ridge; apertural rim prominent. Opercula (Fig. 34) frequently preserved in-situ, surface moderately convex, a flattened median proximal area often evident, bearing about 25 elongate pseudopores in a crescent close to the lateral/distal edge. Autozooids and more commonly small eleozooids (Fig. 31) may be budded intramurally within autozooids. Terminal diaphragms, located below level of apertural shelf, very occasionally present.

Eleozooids (Figs 29, 39–40) abundant, most positioned close to branch margins, especially in the recesses of branch divisions, small examples often associated with occluded growing edges. Frontal walls generally a little narrower than those of autozooids, with a similar concentration of pseudopores. Apertures variable in length, most are long, about 3 × longer than wide, tapering distally with concave lateral edges and a well-developed shelf-like rostrum (typical rostrozooids), but these grade into others which are short and subtriangular; maximum apertural width attained at hinge line level. Opercula not observed. Intramural budding of small eleozooids within large eleozooids (Fig. 40) is common, the rostrum being infilled by pseudoporous exterior wall.

Kenozooids of varying size and shape common, mainly located at occluded growing edges, in recesses of branch divisions and in encrusting bases.

Gonozooids (Figs 41–43) common, sometimes more than one per branch fragment. Distal frontal wall emerging from maternal aperture initially parallel-sided, often for a considerable distance, before becoming densely pseudoporous, bulbous and longitudinally ovoidal in shape. Ooeciopore positioned beyond inflated part of frontal wall, transversely elliptical, about one-and-a-half times as wide as long, an internal hemiseptum indenting the proximal edge to give a kidney-shaped deep outline. Atrial ring present in at least some gonozooids.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10451)

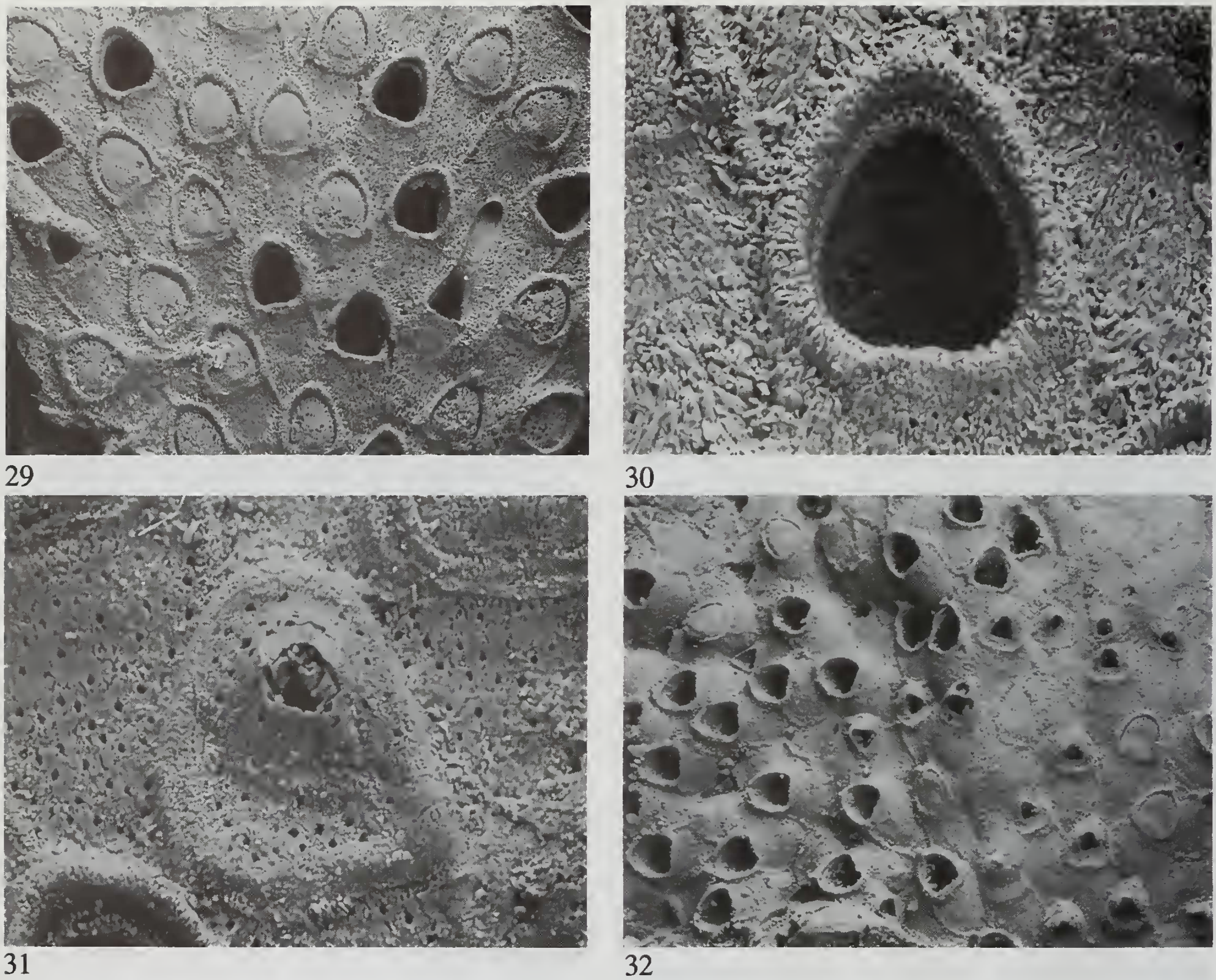
frontal length:	mean = 0·46 mm; SD = 0·026 mm; CV = 5·5; range = 0·42–0·51 mm
frontal width:	mean = 0·23 mm; SD = 0·008 mm; CV = 3·4; range = 0·23–0·24 mm
apertural length:	mean = 0·17 mm; SD = 0·010 mm; CV = 6·1; range = 0·17–0·20 mm
apertural width:	mean = 0·15 mm; SD = 0·009 mm; CV = 6·5; range = 0·14–0·17 mm

eleozooids (10 zooids from holotype VH 10451)

frontal length:	mean = 0·60 mm; SD = 0·139 mm; CV = 23·1; range = 0·32–0·74 mm
frontal width:	mean = 0·20 mm; SD = 0·020 mm; CV = 10·0; range = 0·17–0·23 mm
apertural length:	mean = 0·32 mm; SD = 0·092 mm; CV = 29·3; range = 0·12–0·41 mm
apertural width:	mean = 0·09 mm; SD = 0·012 mm; CV = 12·7; range = 0·08–0·11 mm

gonozooids (10 zooids from holotype VH 10451 and un-numbered VH specimens)

frontal length:	mean = 1·69 mm; SD = 0·227 mm; CV = 13·4; range = 1·29–2·03 mm
dilated frontal length*:	mean = 1·06 mm; SD = 0·162 mm; CV = 15·2; range = 0·74–1·31 mm



Figs 29–32 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany. 29–30, VH 10451, holotype; 29, autozooids (some with opercula) and eleozooids, × 60; 30, autozooidal aperture, × 250. 31, VH 10452, small intramural eleozooid with partially preserved operculum, × 250. 32, VH 10473, autozooids, small primary eleozooids, intramural eleozooids and kenozooids in encrusting colony base, × 42.

frontal wall width: mean = 0·83 mm; SD = 0·134 mm; CV = 16·2; range = 0·63–1·01 mm
ooeciopore length: mean = 0·08 mm; SD = 0·011 mm; CV = 12·8; range = 0·06–0·09 mm
ooeciopore width: mean = 0·14 mm; SD = 0·019 mm; CV = 13·2; range = 0·12–0·18 mm
(* i.e. that part of the frontal wall beyond the narrow, tubular proximal frontal wall)

REMARKS. Particularly characteristic of this species are the long and narrow eleozooidal apertures and the thick autozooidal apertural rims. *E. elegantula* resembles *E. hexagona* d'Orbigny, 1853, from the Santonian but lacks the tubercle developed distally of the autozooidal aperture, and has frontal walls which occupy a larger proportion of the autozooidal frontal area. It is also very similar to the late Cenomanian/Turonian species *E. subhexagona* sp. nov. but has somewhat smaller zooids with relatively more extensive frontal walls. *E. mackinneyi* sp. nov., which occurs with *E. elegantula* at Mülheim/Ruhr, differs in having broad eleozooidal apertures and more rounded autozooidal apertures.

DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Germany.

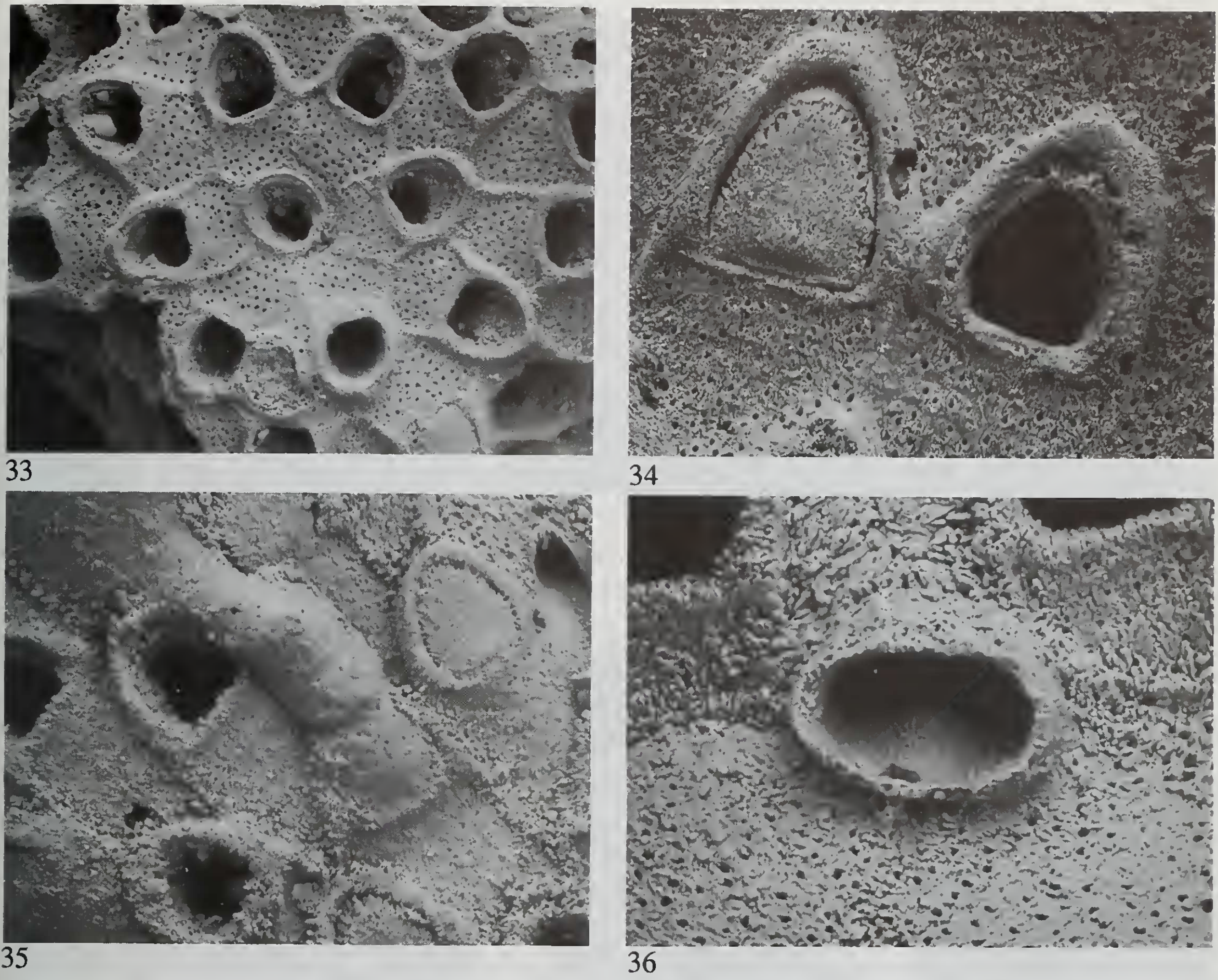
Elea flabellata sp. nov. Figs 44–48

MATERIAL. Holotype: VH 10448, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany. Other material: VH unnumbered, 3 abraded fragments from the same horizon and locality probably belong to this species.

NAME. Flabellum, fan (L.), with reference to the flabellate shape of the holotype colony.

DESCRIPTION. Colony bifoliate, consisting in the holotype of a single non-bifurcating, flabellate branch, 3·2 mm wide proximally, expanding to a width of 14 mm distally, about 1·5 mm thick, distinctly elliptical in cross-section at the proximal fracture. Autozooids arranged in approximate quincunx; organization fixed-walled. Colony base and overgrowths not observed.

Autozooids (Figs 44–45) of small size, frontally a little less



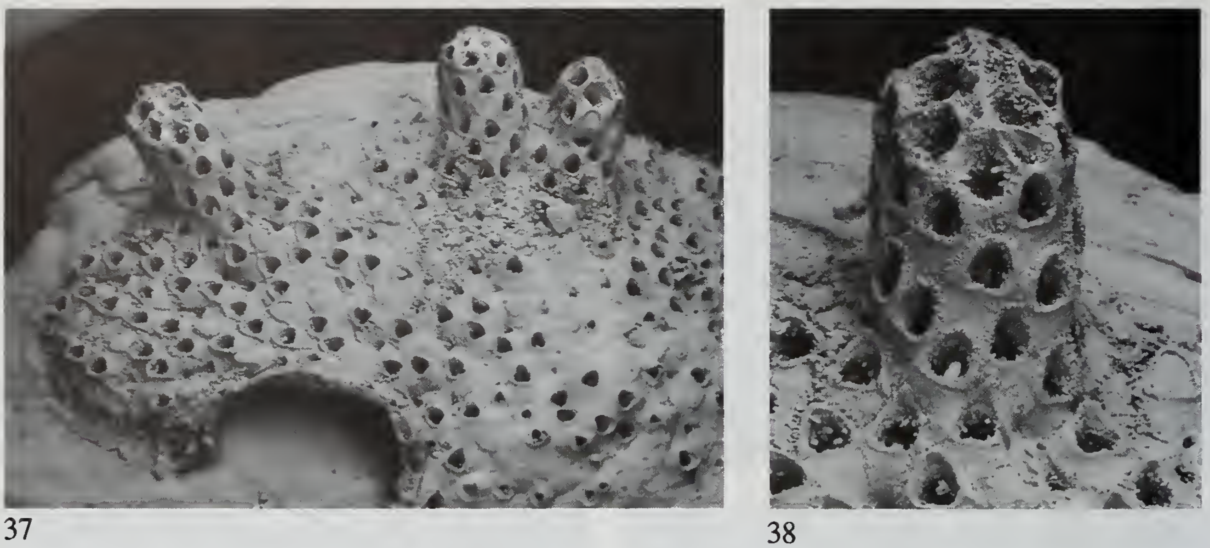
Figs 33–36 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany. 33, VH 10452, overgrowth origin, × 85. 34, VH 9848, operculate autozooid (left) and autozooid containing intramural autozooid (right), × 115. 35, VH 9847, proximal part of a gonozooid showing tubular frontal wall emerging from an autozooid-like aperture, × 75. 36, VH 10451, ooeciopore, × 245.

than twice as long as wide and typically hexagonal in outline shape; zooidal boundaries marked by a broad raised area of calcification prolonged into low, blunt tubercles at the corners of zooids; frontal wall pseudoporous, occupying a very small proportion of the frontal surface (Fig. 47), considerably smaller than the autozooidal apertures. Apertures (Fig. 47) medium-sized, slightly longitudinally elongate or equidimensional, attaining maximum width at about mid-length, well-rounded distally; apertural shelf narrow; hinge line with a median bar. Opercula (Fig. 46) occasionally preserved in-situ, surface convex; pseudopores radially elongate, present over entire surface of operculum. Terminal diaphragms not observed. Intramurally budded autozooids (Fig. 45) infrequent, equipped with a thin, raised secondary apertural rim.

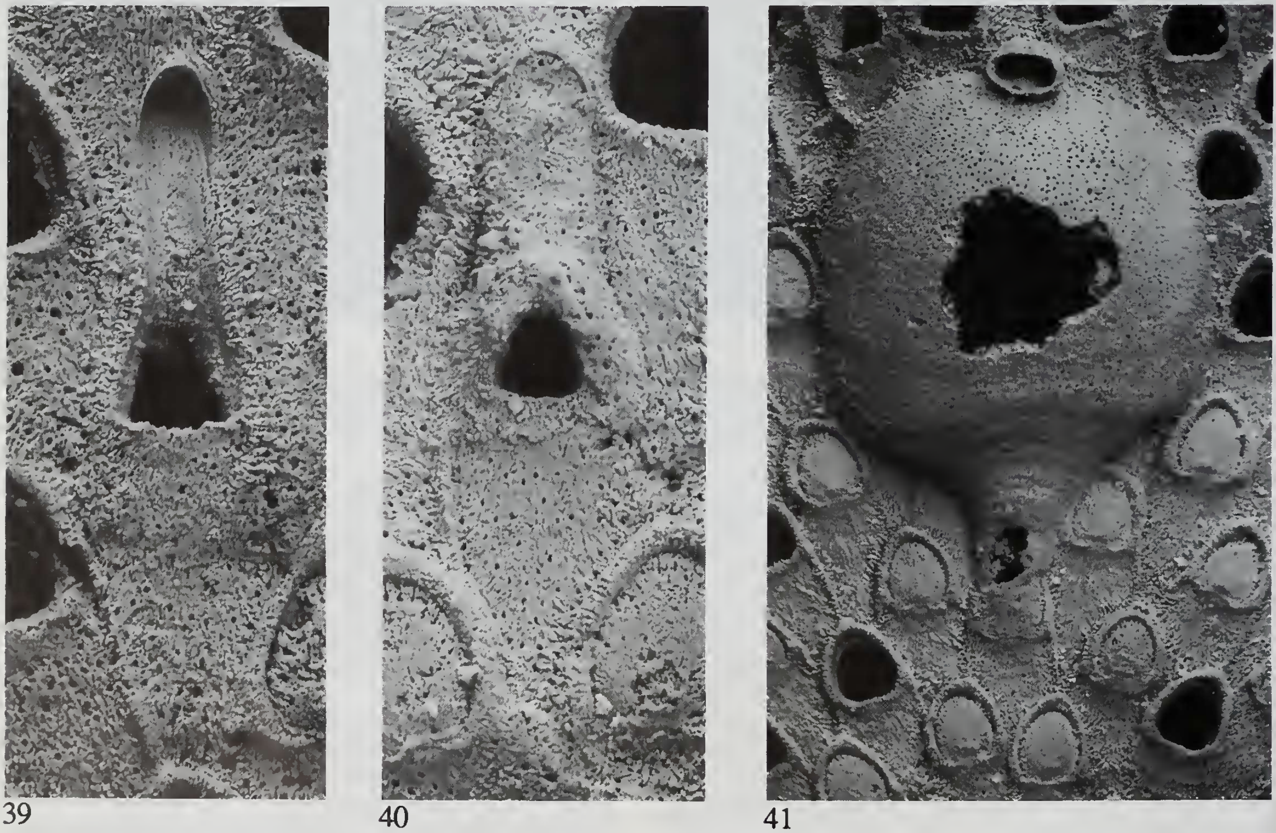
Eleozooids (Fig. 48) abundant, scattered, not concentrated at branch margins, frontally on average 1·8 × longer than wide and about 1·5 × the size of an autozooid; frontal wall pseudoporous, occupying a small proportion of the frontal surface but larger than an autozooidal frontal wall. Aperture moderately elongate, about 1·5 × longer than wide, widest at the hinge line, tapering distally to form a narrow, parallel-sided rostrum which is approximately half the total length of the aperture, rounded distally. Opercula observed in-situ. Intramurally budded autozooids possibly present but rare; intramural eleozooids common, many with apertures facing proximally in a plane oblique to that of the host aperture.

Gonozooids represented by a single example which is both abraded and incompletely formed; longitudinally elongate in outline; ooeciopore and atrial ring not observed.

REMARKS. Only a single adequately-preserved fragment is known of this species. However, the specimen is sufficiently different from other species of *Elea* to be confident that it represents a new species. Although the eleozooids of *E. flabellata* are similar to those present in several other species of *Elea* (e.g. *E. labyrinthica* (Michelin) and *E. hexagona* d'Orbigny), the thick tuberculate calcification which surrounds these as well as the autozooids is very characteristic of the species, as are the much reduced frontal walls. The distribution of pseudopores over the entire surface of the autozooidal operculum is a feature apparently unique to *E. flabellata* among species of *Elea*, although it is present in some species of *Meliceritites* (notably *M. dollfusi* Pergens)



Figs 37, 38 *Elea elegantula* sp. nov., VH 10473, Lower Cenomanian, Mülheim/Ruhr, Germany; 37, colony base encrusting a shell, giving rise to three erect branches (upper left and right) and forming an arch (lower centre) probably where a soft-bodied organism was overgrown, × 17; 38, base of erect branch, × 50.

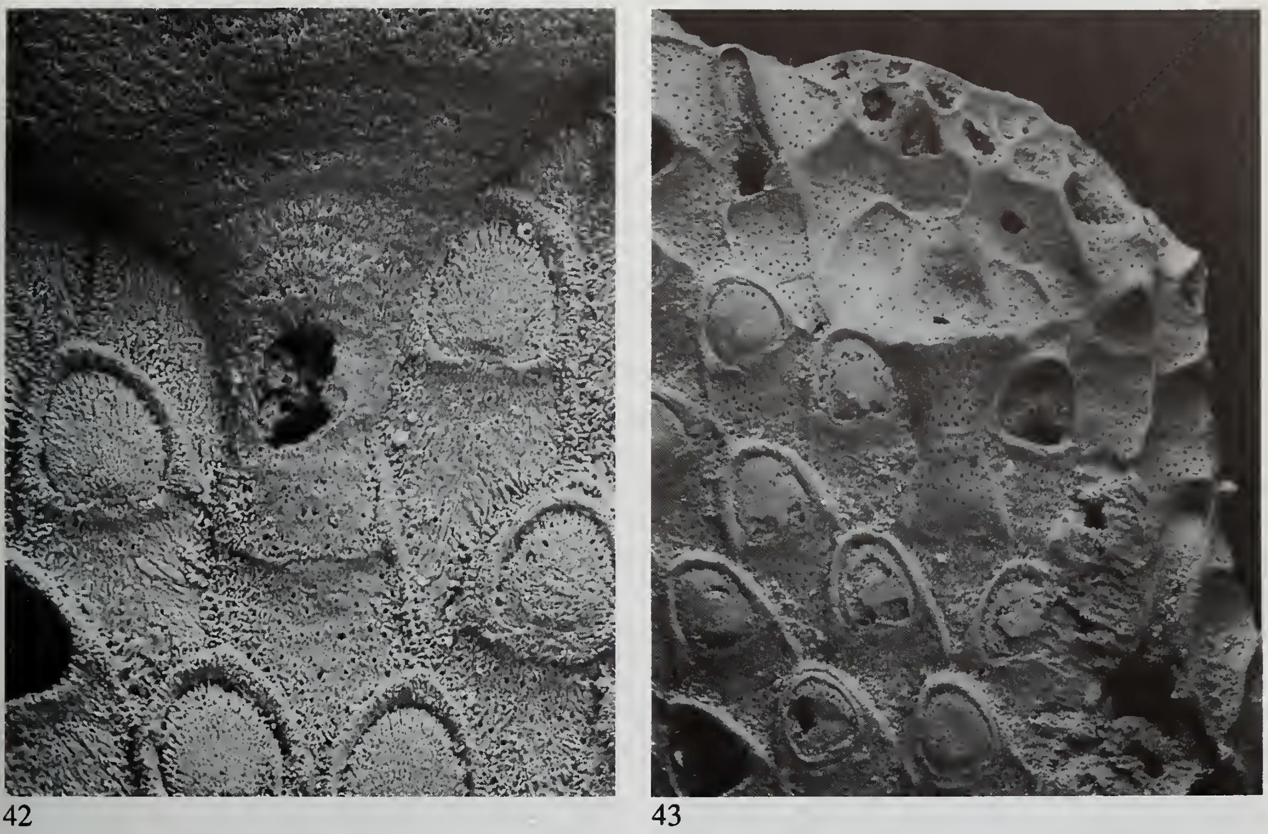


Figs 39–41 *Elea elegantula* sp. nov., VH 10451, Lower Cenomanian, Mülheim/Ruhr, Germany; 39, large eleozooid, × 160; 40, large eleozooid containing small intramural eleozooid, × 145; 41, gonozooid with broken roof, × 65.

and in *Reptomultelea scanica* sp. nov. *E. flabellata* bears a resemblance to *Biforicula nodulifera* (Voigt), also from the Santonian of West Germany. Abraded examples of these two species could be difficult to tell apart were it not for the rather more pointed apertures of *B. nodulifera*.

DISTRIBUTION. Lower Santonian of Broistedt, Germany.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 10448)



Figs 42, 43 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany 42, VH 10451, inflated frontal wall of gonozooid emerging from an autozooid-like aperture, × 145. 43, VH 10452, gonozooid at the edge of a branch which was apparently aborted after growing the proximal part of the inflated frontal wall; zooids which would have formed the floor of the gonozooid are sealed by exterior walls, × 80.

frontal length:	mean = 0·41 mm; SD = 0·027 mm; CV = 6·7; range = 0·36–0·45 mm
frontal width:	mean = 0·27 mm; SD = 0·015 mm; CV = 5·8; range = 0·24–0·29 mm
apertural length:	mean = 0·21 mm; SD = 0·010 mm; CV = 4·9; range = 0·20–0·23 mm
apertural width:	mean = 0·20 mm; SD = 0·007 mm; CV = 3·6; range = 0·20–0·21 mm

eleozooids (10 zooids from holotype VH 10448)

frontal length:	mean = 0·66 mm; SD = 0·048 mm; CV = 7·3; range = 0·57–0·75 mm
frontal width:	mean = 0·36 mm; SD = 0·020 mm; CV = 5·5; range = 0·35–0·39 mm
apertural length:	mean = 0·40 mm; SD = 0·042 mm; CV = 10·5; range = 0·33–0·45 mm
apertural width:	mean = 0·27 mm; SD = 0·018 mm; CV = 6·6; range = 0·26–0·30 mm

gonozooid (abraded, incomplete zooid from holotype VH 10448)

total frontal length:	>1·73 mm
frontal width:	*ca* 1·28 mm

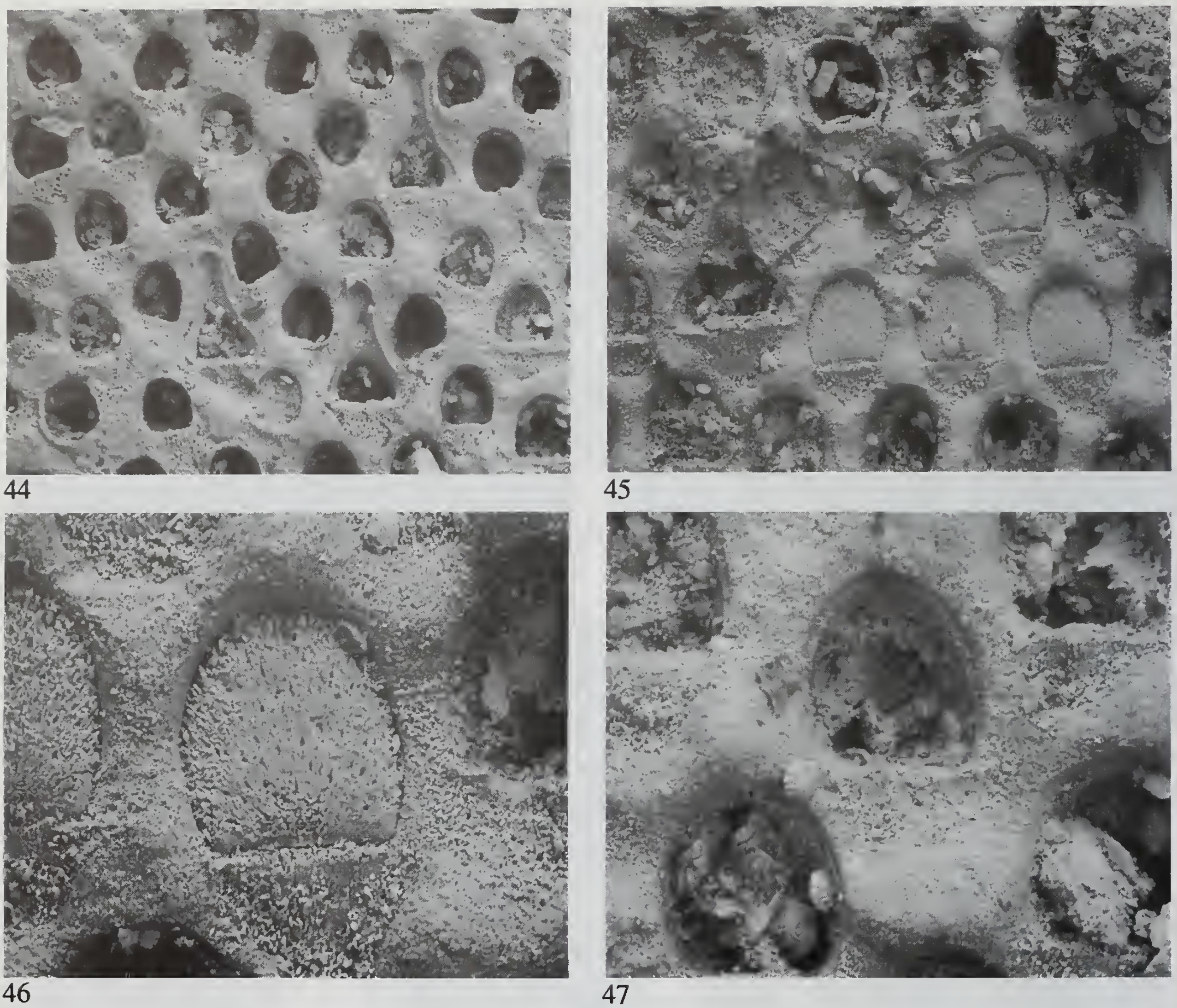
Elea hexagona d'Orbigny, 1853 Figs 49–56

1853 *Elea hexagona* d'Orbigny: 633, pl. 738, figs 1–4.
1889 *Elea hexagona* d'Orbigny; Pergens: 398.
non 1897 *b* *Elea hexagona* d'Orbigny; Canu: 753.
1899 *Elea hexagona* (d'Orbigny); Gregory: 303.
1912 *Meliceritites hexagona* (d'Orbigny); Levinsen: 43, pl. 5, figs 3–5.

Material. Lectotype (herein designated): MNHN d'Orbigny Collection 8192 (Fig. 49), fragment in tube labelled 'Type' by E. Voigt (Voigt photocard 5791), Senonian [Santonian], Vendôme, Loir-et-Cher, France. Paralectotype: one of the two other fragments registered with lectotype as MNHN 8192 (the third fragment is ?*Foricula*). Other material: ZMC Levinsen Colln M38 and M39, Santonian, Vendôme, France; ZMC Levinsen Colln, about ten un-numbered topotypes.

Description. Colony bifoliate with branches (Figs 49–50) bifurcating, strap-like, narrow, about 1·7–2·3 mm wide. Autozooids usually arranged in approximate quincunx; organization fixed-walled. Colony base not observed. Overgrowths produced by eruptive budding onto the branch surface present.

Autozooids (Fig. 51) moderately large; frontal surface usually hexagonal with edges parallel to long axis or diamond-shaped, elongate, about twice as long as wide; frontal wall small in area, with subcircular pseudopores; zooecial boundaries formed mainly by apertural rims, raised. Apertures (Fig. 52) medium-sized, longitudinally elongate, about 1·2 × longer than wide, attaining maximum width



Figs 44–47 *Elea flabellata* sp. nov., VH 10448, holotype, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany; 44, autozooids and three eleozooids, × 50; 45, autozooids, an eleozooid, and an intramural autozooid (top centre left), × 70; 46, autozooidal operculum, × 200; 47, autozooidal aperture and reduced frontal wall, × 160.

between hinge line and mid-length, rounded distally; apertural shelf variably developed; apertural rim moderately prominent proximally, distally forming a conspicuous, deep tubercle; hinge line bowed. Opercula (Fig. 56) often preserved in-situ, surface convex, pseudopores not evident in poorly-preserved available material. Terminal diaphragms not observed. Intramurally budded autozooids (Figs 52–53) common, some having apertures in same plane as host aperture but significantly smaller and more rounded distally, others having apertures in an oblique plane facing proximally relative to branch orientation and possessing a very prominent tubercle distal to the aperture.

Eleozooids (Figs 51, 53–54) abundant, located particularly at branch margins and in bifurcations, about 2·5–3 × longer than wide, frontally slightly wider and significantly longer than autozooids. Aperture elongate, about 2–2·5 × longer than wide, attaining maximum width at the hinge line and tapering distally to a long, narrow rostrum with a rounded end. Opercula not observed in-situ.

Gonozooid unknown.

MEASUREMENTS (estimated from SEM micrographs).

autozooids	
frontal wall length:	*ca* 0·43–0·50 mm
frontal wall width:	*ca* 0·22–0·26 mm
apertural length:	*ca* 0·18–0·21 mm
apertural width:	*ca* 0·16–0·18 mm
eleozooids	
frontal wall length:	*ca* 0·62–0·83 mm
frontal wall width:	*ca* 0·25–0·27 mm
apertural length:	*ca* 0·36–0·50 mm
apertural width:	*ca* 0·17–0·23 mm

REMARKS. The supposed *Elea hexagona* described by Canu (1897*b*) from the Cenomanian of Saint-Calais is here included in *E. subhexagona* sp. nov. This species more closely resembles *E. hexagona* than any other species of *Elea* but lacks the very deep and prominent tubercle distal to the

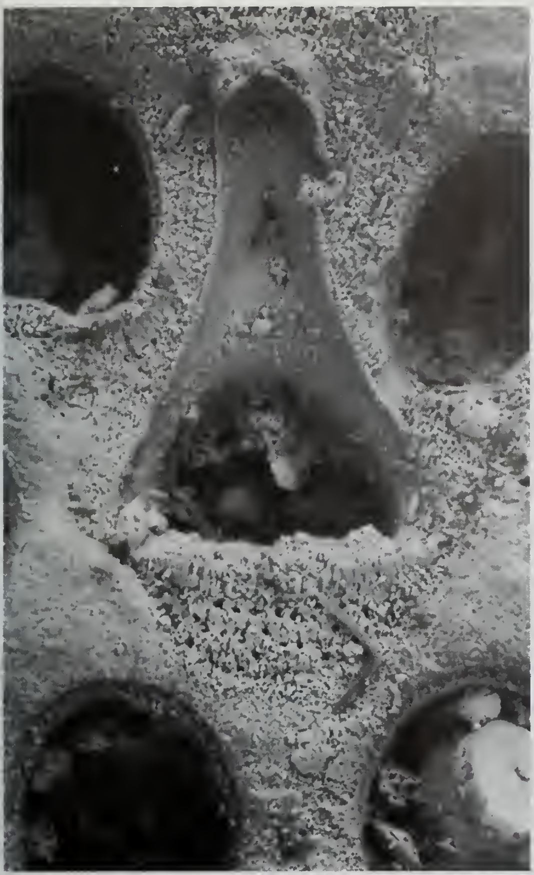


Fig. 48 *Elea flabellata* sp. nov., VH 10448, holotype, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany; eleozooid, × 185.

autozooidal aperture, which is a characteristic feature of *E. hexagona*. The larger size of the autozooidal apertures enables distinction between *E. hexagona* and *E. labyrinthica*. Filliozat (1908) records *E. hexagona* from the Calcaire graveleux, Assise á *Crania ignabergensis*, Craie de Vendôme. Unfortunately, the species is unrepresented in both the BMNH and VH collections.

DISTRIBUTION. Santonian of Vendôme, Loir-et-Cher, France.

Elea labyrinthica (Michelin, 1843) Figs 57–65

1843 *Eschara labyrinthica* Michelin: 124, pl. 32, fig. 2.
1843 *Eschara neustriaca* Michelin: 124, pl. 32, fig. 3.
1853 *Elea rhomboidalis* d'Orbigny: 631, pl. 737, figs 21–24.
1890 *Elea rhomboidalis* d'Orbigny; Pergens: 399.
1899 *Elea labyrinthica* (Michelin); Gregory: 303.
1899 *Elea rhomboidalis* d'Orbigny; Gregory: 304.

MATERIAL. Type: the syntypes of this species (and of the contemporaneous *Eschara neustriaca*) are not among the Michelin types in the MNHN (see Walter 1975); Michelin (1843) gives Cap de la Hève, Honfleur, Villers-sur-Mer and Vaches-Noires as localities, and Craie Chloritée [= Craie Glauconieuse, Lower Cenomanian] as the horizon. Other material: MNHN d'Orbigny Collection 6627 [= Voigt photocard 7475] (presumed type specimen of *E. rhomboidalis*), Cenomanian, Le Havre, France; BMNH D31139, VH 10460, Cenomanian, Cap de la Hève, Seine Maritime, France; BMNH D58900–2, Lower Cenomanian, Craie Glauconieuse, Cap de la Hève; BMNH D58763–4, D58890–2, Craie Glauconieuse, Port d'Antifer, Seine Maritime, France; BMNH D59156 (sample), Craie Glauconieuse, Villers-sur-Mer, Calvados, France; BGS GSM 118097-8, Lower Cenomanian, Warminster Greensand, Warminster, Wiltshire, England, Cunnington Collection; BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; BMNH D59157, Cenomanian Limestone, Bed A1 (*mantelli* Zone), The Pinnacles, near Beer, Devon; BMNH D59158, Cenomanian (float), White Hart Sandpit, Wilmington, Devon. VH unnumbered specimens, Lower Cenomanian (*carcitanensis* Zone), Carriére du Billot, Notre-Dame-de-Fresnaye, Calvados, collected by G. Breton.

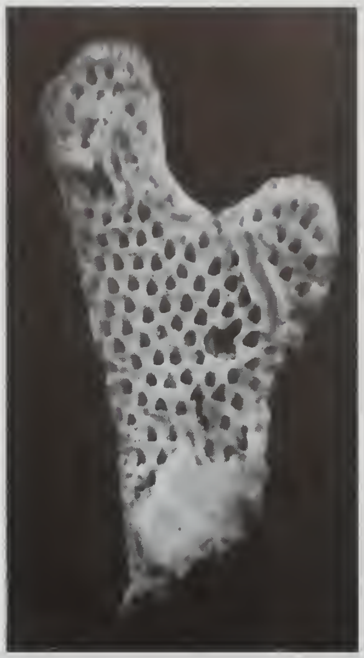


Fig. 49 *Elea hexagona* d'Orbigny, 1853, photograph of MNHN d'Orbigny Collection 8192 (Voigt photocard 5791), lectotype, Senonian [Santonian], Vendôme, Loir-et-Cher, France; colony is fouled by serpulids and an oyster; × 10.

DESCRIPTION. Colony bifoliate with branches of variable morphology, strap-like, bifurcating and about 6 mm wide in some specimens, broad and folded in others (e.g. Michelin 1843, pl. 32, fig. 2); branches about 0·9 mm deep. Zooids arranged in regular to approximate quincunx (Figs 57, 61); organization fixed-walled. Overgrowths extremely common, originating through eruptive budding onto the surfaces of erect branches; growing edges of overgrowths sometimes closed by terminal diaphragms. Colony base extensive, giving rise to more than one erect branch. Possible conspecific ancestrula adjacent to a gonozooid in VH 10460 has a very short distal tube and large protoecium about 0·22 mm wide.

Autozooids (Figs 57, 61–62) medium-sized, with frontal walls elongate, over twice as long as wide, typically hexagonal but occasionally diamond-shaped, pierced by circular to

Fig. 50 *Elea hexagona* d'Orbigny, 1853, ZMC Levinsen Collection M39, Santonian, Vendôme, France, × 28.

slightly longitudinally elongate pseudopores; zooidal boundaries marked by low, thread-like ridges. Apertures (Fig. 59) small, longitudinally elongate, a little less than 1·5 × longer than wide, attaining maximum width about mid-length, rounded distally; apertural shelf distinct, narrow; hinge line very slightly bowed, teeth not clearly apparent; apertural rim raised. A large and prominent tubercle (Fig. 61) occurs distally of the autozooidal aperture and is shaped like a compressed barkhan dune facing towards the aperture. Opercula (Fig. 58) fairly commonly found in-situ, surface convex, bearing about 10 radial ridges peripheral to a central flatter area; pseudopores not seen. Intramural eleozooids often present; apertures variably D-shaped to inverted T-shaped, located within the distal half of the aperture of the host autozooid. Intramural autozooids possibly present but infrequent.

Eleozooids (Figs 57, 60, 62–64) common, scattered or in small groups, with pseudoporous frontal walls having approximately the same area as, though often narrower than, those of autozooids. Apertures highly variable in length, ranging from about 2 to 5 × longer than wide, tapering to become very narrow at the rounded distal extremity; apertural shelf wide, beginning just distally of the hinge-line; distal tubercle absent. Opercula (Fig. 63) occasionally found in-situ. Intramural eleozooids (Fig. 64) often present.

Gonozooids known from only one specimen (VH 10460), which has an intact and an abraded example; in the former (Fig. 65) an initially narrow, tubular distal frontal wall becomes densely pseudoporous before dilating into an elongate ovoid shape. Ooeciopore circular or slightly longitudinally elongate, about the same length as an autozooidal aperture. Atrial ring not apparent in the abraded gonozooid, in which the vertical walls of the more proximally overgrown zooids protrude from the floor of the gonozooid, whereas those of the more distal zooids do not.

MEASUREMENTS.
autozooids
(10 zooids with in-situ opercula from BGS GSM Rh 4582)

frontal length:	mean = 0·55 mm; SD = 0·033 mm; CV = 6·1; range = 0·50–0·60 mm
frontal width:	mean = 0·22 mm; SD = 0·023 mm; CV = 10·2; range = 0·18–0·26 mm
apertural length:	mean = 0·14 mm; SD = 0·014 mm; CV = 10·1; range = 0·12–0·17 mm
apertural width:	mean = 0·10 mm; SD = 0·010 mm; CV = 10·6; range = 0·08–0·11 mm

(10 zooids from BMNH D31139)

frontal length:	mean = 0·58 mm; SD = 0·043 mm; CV = 7·4; range = 0·53–0·63 mm
frontal width:	mean = 0·25 mm; SD = 0·016 mm; CV = 6·3; range = 0·23–0·27 mm
apertural length:	mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·14–0·17 mm
apertural width:	mean = 0·11 mm; SD = 0·007 mm; CV = 6·7; range = 0·09–0·12 mm

eleozooids (5 zooids from BGS GSM Rh 4582; 5 zooids from BMNH D31139)

frontal length:	range = 0·42–1·02 mm
frontal width:	range = 0·17–0·27 mm
apertural length:	range = 0·20–0·54 mm
apertural width:	range = 0·06–0·09 mm

gonozooid (VH 10460)

total frontal length:	2·72 mm
distal frontal wall length:	2·51 mm
frontal wall width:	0·98 mm
ooeciopore length:	0·11 mm
ooeciopore width:	0·11 mm

REMARKS. Although type material is lacking, the identity of this species is not in doubt as Michelin's enlarged figure (1843: pl. 32, fig. 2b) shows very clearly the prominent tubercles located distally of the autozooidal apertures. In no other meliceritítid species are the distal tubercles so well-developed or shaped so much like barkhan dunes.

Specimens of *E. labyrinthica* from the type horizon – the Craie Glauconieuse, where it is very common, exhibit variable colony forms, some being adeoniform while others are eschariform. One specimen (BMNH D58763) encrusts a sponge.

DISTRIBUTION. Lower Cenomanian of northern France and south-west England; known from sandy facies only.

Elea mackinneyi sp. nov. Figs 66–71

MATERIAL. Holotype: VH 10474, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. Paratypes: VH 10541 (4

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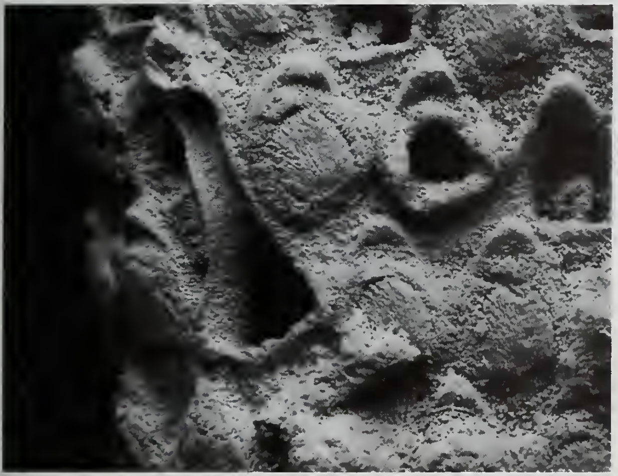

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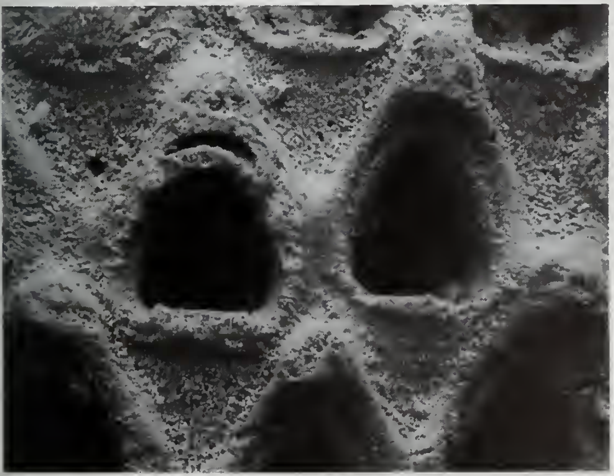

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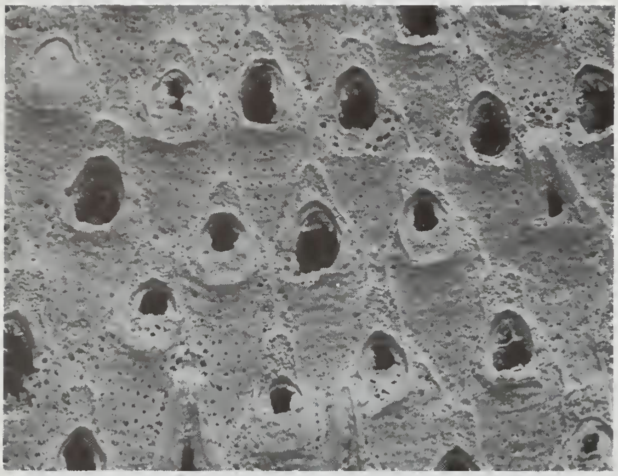
Figs 51–56 *Elea hexagona* d'Orbigny, 1853, Santonian, Vendôme, France. 51–54, ZMC Levinsen Collection M38; 51, autozooids and a marginal eleozooid (lower left), × 33; 52, intramural operculate autozooid (left) and autozooidal aperture (right), × 135; 53, marginal eleozooid and intramural autozooids, × 70; 54, non-marginal eleozooid, × 98. 55, 56, ZMC M39; 55, intramural autozooid (left) and normal autozooid (right), × 135; 56, autozooidal operculum, × 150.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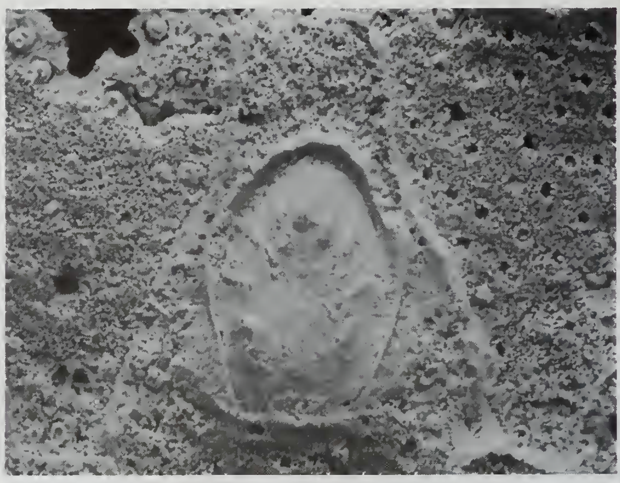
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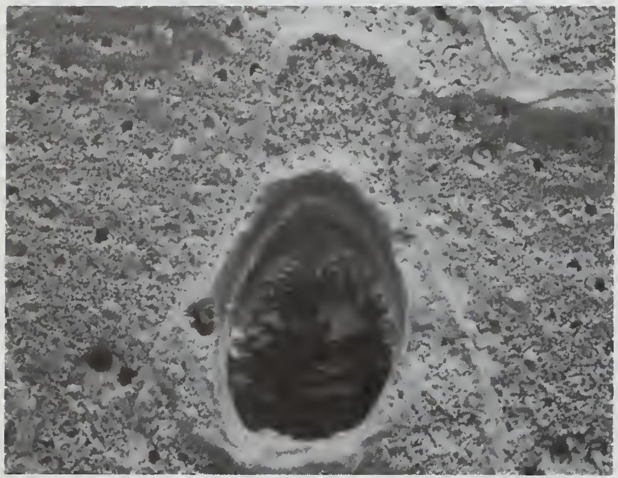
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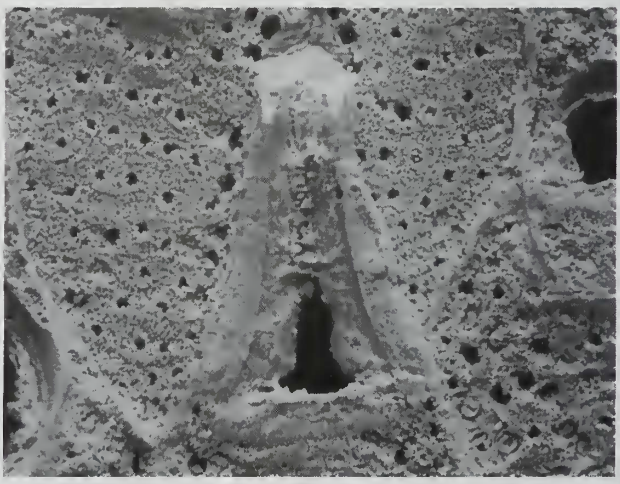
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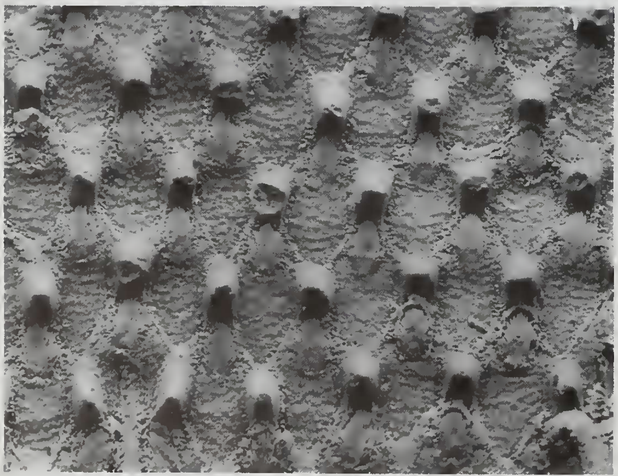
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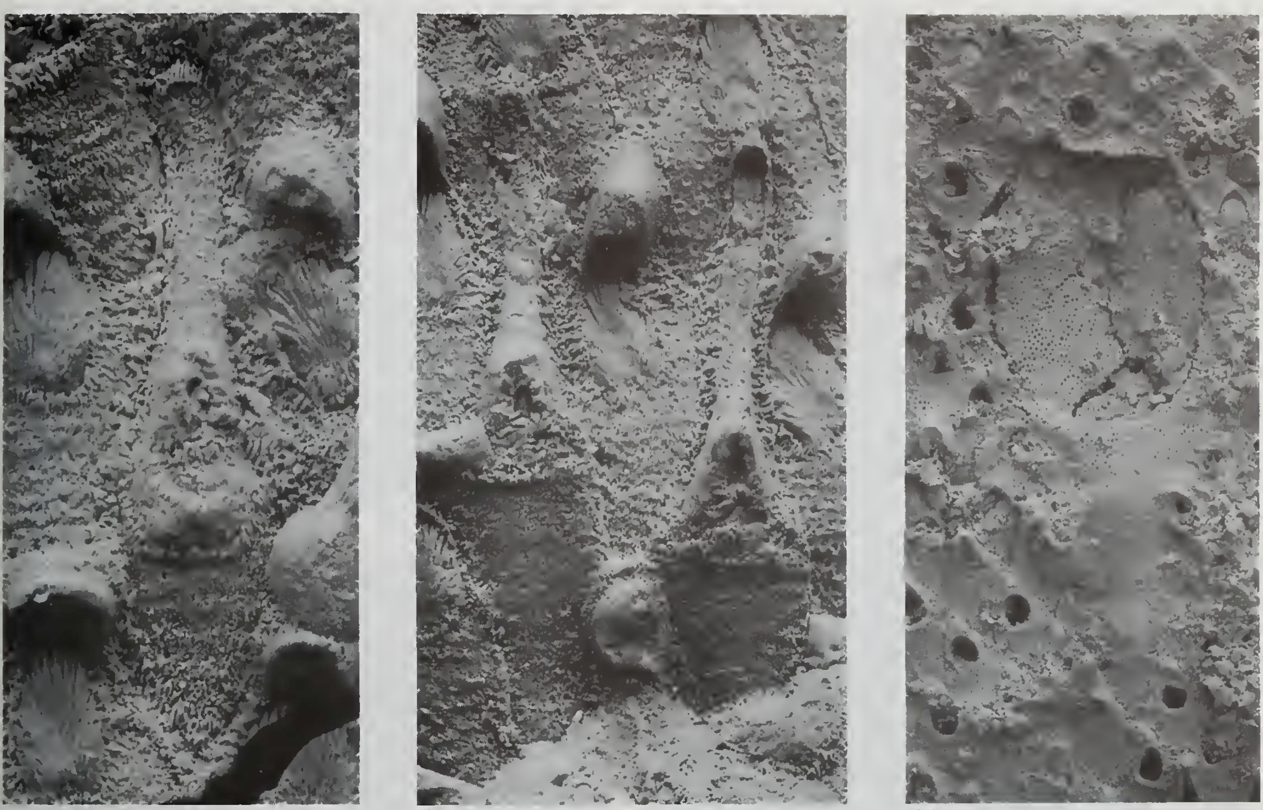
Figs 57–62 *Elea labyrinthica* (Michelin, 1843). 57–60, BMNH D31139, Cenomanian, Cap de la Hève, Seine Maritime, France; 57, autozooids, eleozooids and intramural eleozooids; distal tubercles abraded, × 55; 58, autozooidal operculum, × 170; 59, autozooidal aperture, × 185; 60, eleozooid with distally broken rostrum, × 175. 61, 62, BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; 61, autozooids with prominent distal tubercles, × 48; 62, autozooids and eleozooids with long, narrow rostra, × 70.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Figs 63–65 *Elea labyrinthica* (Michelin, 1843). 63, 64, BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; 63, large eleozooid with slightly damaged operculum, × 145; 64, two large eleozooids housing small intramural eleozooids, × 110. 65, VH 10460, Cenomanian, Cap de la Hève, Seine Maritime, France, gonozooid with crushed frontal wall, × 35.

specimens), same horizon and locality as holotype.

Name. In recognition of the numerous fundamental contributions made to bryozoology by Dr F.K. McKinney (Appalachian State University).

Description. Colony bifoliate with branches (Fig. 66) narrow, strap-like, about 1·8 mm wide between bifurcations, and 0·7 mm deep. Autozooids generally arranged in transverse rows whose regularity is disrupted close to bifurcations; organization fixed-walled. Overgrowths and colony base not observed.

Autozooids (Fig. 67) medium-sized, with elongate hexagonal frontal walls on average slightly less than 2 × longer than wide; pseudopores circular or longitudinally elliptical; zooecial boundaries raised. Apertures small, longitudinally elongate, about 1·1 × longer than wide, attaining maximum width a little proximally to mid-length, appreciably narrower at hinge line level; apertural shelf absent or at most very slightly developed; apertural rim moderately raised; hinge line straight or slightly bowed, typically concave in eroded zooids lacking opercula. Opercula (Fig. 69) rarely preserved in-situ, flat or slightly depressed, bearing about 16 pseudopores arranged in a crescent parallel to the distal/lateral margin. Terminal diaphragms not observed. Intramurally budded autozooids represented by a single example with a slightly oblique aperture (Fig. 70).

Eleozooids (Figs 67, 68) common, located along branch margins, on average about 3 × longer than wide, usually occupying two transverse rows of autozooids. Aperture long, widest at the hinge line but broad throughout, sometimes very slightly spatulate, well-rounded distally, on average twice as long as wide. In-situ opercula and intramural buds not observed.

Kenozooids (Fig. 68) occasionally present at branch margins, especially within bifurcations.

Gonozooids (Fig. 71) of unknown abundance (one fully developed and one partially developed example present in holotype VH 10474); distal frontal wall dilating soon after emerging from maternal aperture, longitudinally ovoidal in shape, about 2 × longer than wide. Ooeciopore not observed. Atrial ring present.

Measurements.

autozooids (10 zooids from holotype VH 10474)

frontal length:	mean = 0·49 mm; SD = 0·029 mm; CV = 6·0; range = 0·45–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·018 mm; CV = 6·7; range = 0·24–0·29 mm
apertural length:	mean = 0·18 mm; SD = 0·006 mm; CV = 3·6; range = 0·17–0·18 mm
apertural width:	mean = 0·16 mm; SD = 0·005 mm; CV = 2·9; range = 0·15–0·17 mm

eleozooids (10 zooids from holotype VH 10474)

frontal length:	mean = 1·00 mm; SD = 0·184 mm; CV = 18·5; range = 0·75–1·26 mm

Fig. 66 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; branch with broken gonozooid and fouling foraminifer (top left), × 20.

frontal width: mean = 0·36 mm; SD = 0·050 mm; CV = 13·9; range = 0·30–0·44 mm
apertural length: mean = 0·49 mm; SD = 0·102 mm; CV = 20·7; range = 0·33–0·65 mm
apertural width: mean = 0·24 mm; SD = 0·034 mm; CV = 13·8; range = 0·18–0·29 mm

gonozooid (from holotype VH 10474)
total frontal length: 2·34 mm
dilated frontal wall length: 2·07 mm
frontal wall width: 1·04 mm

REMARKS. Although known from only a few specimens, this is a very distinctive species. The broad shape of the eleozooid rostra serve to distinguish *Elea mackinneyi* from sympatric *Elea elegantula* sp. nov., and it differs from *E. viskovae* sp. nov. from the Turonian of the Kazakhstan in having longer rostra and in lacking an appreciable autozooidal apertural shelf.

DISTRIBUTION. Lower Cenomanian of Germany.

Elea pseudolamellosa sp. nov. Figs 72–78

MATERIAL. Holotype: VH 10462, Upper Campanian, St Severin d'Uzel, Charente Maritime, France. Paratypes: VH 10461, same horizon and locality as holotype; VH 10471, Senonian, La gare de Soullans, Vendée, France. BMNH BZ 441–4 , Upper Campanian, Cailleau, near Talmont, Charente Maritime, France. Other material: VH unnumbered topotypes.

NAME. With reference to its similarity to *Elea lamellosa* (d'Orbigny).

DESCRIPTION. Colony bifoliate, consisting of broad, folded fronds about 0·9 mm deep. Growing edge may be occluded by kenozooids and eleozooids. Colony base not observed. Overgrowths may be present. Zooids arranged in approximate quincunx; organization fixed-walled.

Autozooids (Figs 72, 76) medium-sized, frontally hexagonal in outline, on average 1·6 × as long as wide, distal edge prolonged by aperture; frontal wall slightly convex, with circular pseudopores; zooecial boundary wall inconspicuous, thin, little raised. Apertures (Fig. 74) small, longitudinally elongate, about 1·2 × longer than wide, reaching maximum width a little distally of the hinge line, well-rounded distally; apertural shelf narrow; apertural rim narrow but prominent, continuous with zooecial boundary wall; hinge line bowed. Opercula (Fig. 73) infrequently preserved in-situ, prominent, surface convex, seemingly with radially elongate pseudopores widely distributed. Terminal diaphragms not observed. Intramural eleozooids present, their D-shaped apertures occupying the distal part of the host aperture, which is proximally covered by a slightly concave pseudoporous exterior wall.

Eleozooids (Figs 72, 76–77) common, often clustered, especially near occluded growing edges; frontally variable in size, typically only slightly smaller than autozooids; frontal wall with circular pseudopores. Apertures (Fig. 77) small, D-shaped, equidimensional or transversely elongate. In-situ opercula and intramural buds not observed.

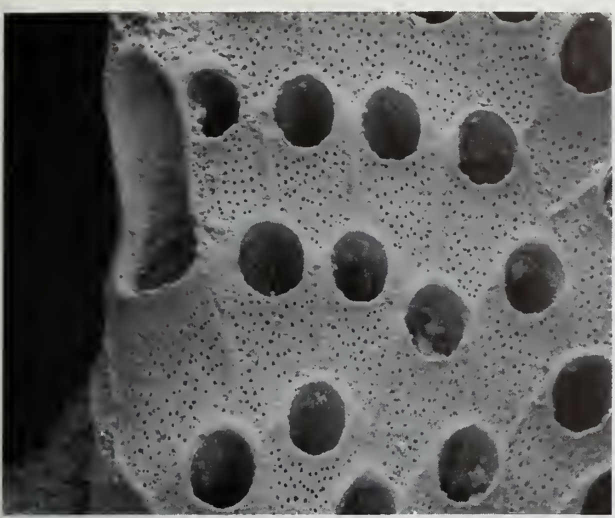
Kenozooids observed in association with eleozooids and gonozooids (Fig. 75).

Gonozooids (Fig. 78) large, longitudinally elongate; frontal wall with a short parallel-sided portion emerging from the maternal zooidal aperture (Fig. 75), dilating into an ovoidal distal portion about twice as long as wide. Ooeciopore not observed (destroyed during abrasion of frontal wall in available specimens). Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids from holotype VH 10462)
frontal length: mean = 0·53 mm; SD = 0·029 mm; CV = 5·6; range = 0·48–0·57 mm
frontal width: mean = 0·33 mm; SD = 0·024 mm; CV = 7·2; range = 0·30–0·38 mm
apertural length: mean = 0·18 mm; SD = 0·014 mm; CV = 7·7; range = 0·17–0·21 mm
apertural width: mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·14–0·17 mm

eleozooids (estimated from SEM micrographs of VH 10461–2)
apertural length: *ca* 0·05–0·07 mm
apertural width: *ca* 0·06–0·07 mm

gonozooid (one zooid from VH 10462)
frontal length: 2·52 mm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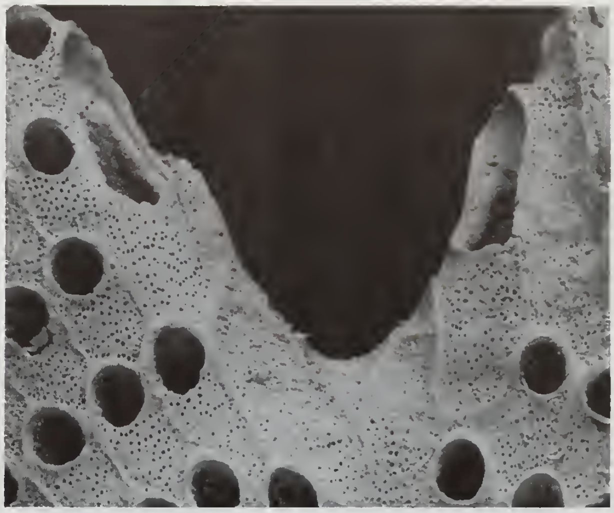
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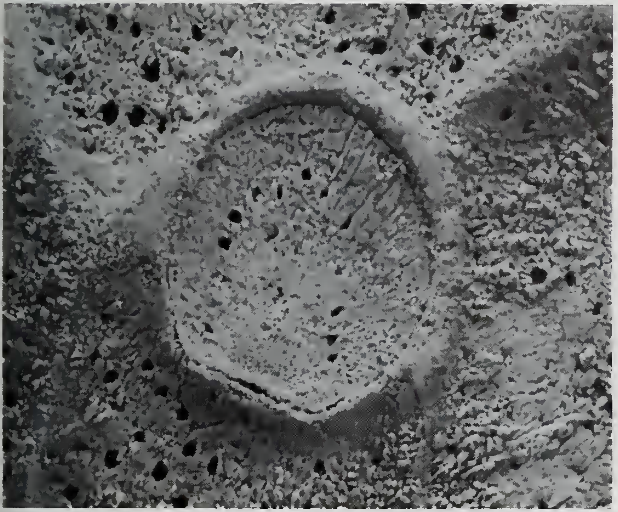
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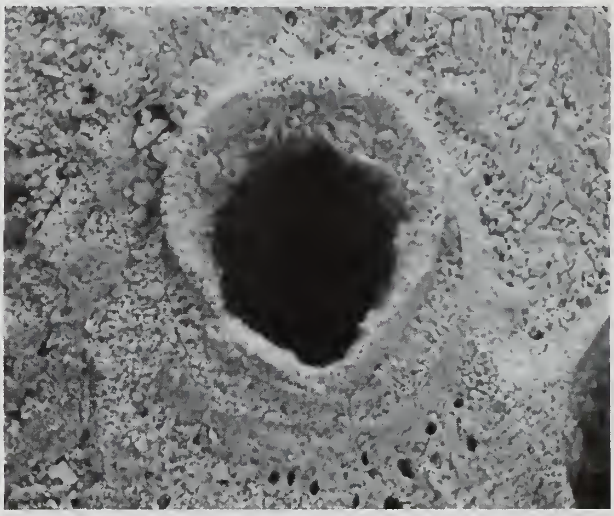
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Figs 67–70 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 67, autozooids and marginal eleozooid, × 55; 68, two marginal eleozooids and kenozooids at a bifurcation, × 44; 69, autozooidal operculum, × 265; 70, oblique intramural autozooidal aperture, × 265.

distal frontal length:	2·31 mm
frontal width:	1·20 mm

REMARKS. This species is extremely similar to *Elea lamellosa* d'Orbigny (see p. 17). The principal point of distinction is the D-shaped form of the eleozooid aperture, which contrasts with the inverted T-shaped aperture characteristic of the eleozooids in *E. lamellosa*. (i.e. the eleozooids of *E. pseudolamellosa* are demizooids, whereas those of *E. lamellosa* are trifoliozooids; compare Figs 77 and 19) This difference appears to reflect the presence of a rostral shelf in *E. lamellosa* which is absent in *E. pseudolamellosa*. Autozooidal frontal walls may be a little more convex and zooecial boundary walls rather less well-developed in *E. pseudolamellosa* than in *E. lamellosa*. The stratigraphical distribution of the two species differs, *E. lamellosa* occurring in the Coniacian-Santonian (and possibly the Turonian), whereas *E. pseudolamellosa* is known with certainty only from the Upper Campanian; a paratype (VH 10471) from the Vendée assigned to *E. pseudolamellosa* is of unknown age within the Senonian.

DISTRIBUTION. Upper Campanian of Charente Maritime, and undifferentiated Senonian of the Vendée, France.

Elea subhexagona sp. nov. Figs 79–86

non 1846 *Escharites dichotoma* Reuss: 66, pl. 15, fig. 31.
1874 *Echarites dichotoma* (Reuss); Reuss: 135, pl. 25, fig. 8.
1897*b* *Elea hexagona* d'Orbigny; Canu: 753.

MATERIAL. Holotype: DM un-numbered, Voigt photocard 2060 (specimen figured by Reuss 1874, pl. 25, fig. 8), Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany. Paratypes: ZMC M53–5, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France. Other material: MNHN Canu Collection unnumbered.

Fig. 71 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; gonozooid with broken frontal wall exposing atrial ring, × 48.

NAME. With reference to the resemblance to *Elea hexagona*.

DESCRIPTION. Colony bifoliate with branches (Fig. 79) bifurcating, strap-like, narrow, about 1·3–2·3 mm wide. Autozooids generally arranged in approximate quincunx; organization fixed-walled. Colony base not observed. Overgrowth present in ZMC M54, consisting of kenozooids spreading between apertures of underlying autozooids, possibly free-walled (Fig. 79).

Autozooids (Figs 80, 81) medium-sized; frontal surface usually hexagonal, elongate, about twice as long as wide; frontal wall occupying about half of frontal surface, flat with circular pseudopores; zooecial boundaries raised. Apertures (Fig. 83) small, longitudinally elongate, on average 1·1–1·2 × longer than wide, attaining maximum width between hinge line and mid-length, rounded distally; apertural shelf narrow; apertural rim well-developed; hinge line with a subdued median bar. Opercula (Fig. 82) often preserved in-situ, surface convex, sometimes with a flattened median area close to the hinge line, pseudopores not visible in studied material. Terminal diaphragms not observed. Intramurally budded autozooids may be present, their apertures typically shorter and more rounded than normal autozooids.

Eleozooids (Figs 84–85) common, especially at branch margins and in bifurcations, about 3–4 × longer than wide, frontally slightly wider but appreciably longer than autozooids. Aperture elongate, about 2–3 × longer than wide, widest at the hinge line and tapering to a long narrow rostrum with a rounded end. Opercula (Fig. 84) observed in-situ, surface convex. Intramurally budded eleozooids (Fig. 81) present.

Kenozooids sometimes present in branch bifurcations.

Gonozooids (Fig. 86) with a short parallel-sided proximal frontal wall emerging from the maternal zooid aperture, becoming longitudinally ovoidal, distal dilated frontal wall approximately 1·5 × longer than wide. Ooeciopore removed by abrasion; atrial ring present.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from the holotype)
frontal length: mean = 0·53 mm; SD = 0·040 mm; CV = 7·6; range = 0·48–0·60 mm
frontal width: mean = 0·27 mm; SD = 0·019 mm; CV = 7·1; range = 0·26–0·30 mm
apertural length: mean = 0·19 mm; SD = 0·007 mm; CV = 4·1; range = 0·18–0·20 mm
apertural width: mean = 0·17 mm; SD = 0·007 mm; CV = 4·3; range = 0·15–0·18 mm

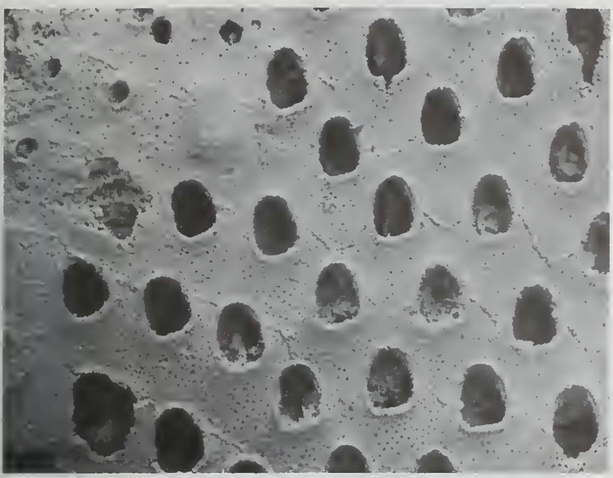
eleozooids (5 zooids from the holotype)
frontal length: range = 0·74–0·81 mm
frontal width: range = 0·23–0·29 mm
apertural length: range = 0·36–0·42 mm
apertural width: range = 0·15–0·20 mm

gonozooids (2 zooids estimated from SEM micrographs of ZMC M53 and M55)
total frontal length: *ca* 1·61–1·88 mm
distal frontal wall length*: *ca* 1·24–1·44 mm
frontal width: *ca* 0·85–0·96 mm
(* i.e. that part of the frontal wall distal to the narrow origin)

REMARKS. This new species was identified by Reuss (1874) as *Escharites dichotoma* Reuss, 1846. Unfortunately, the type specimen of *E. dichotoma*, from the Exogyrensandstein of Bohemia, was destroyed in 1956 (E. Voigt pers. comm. December 1986). However, it is clear from the figure of Reuss (1846), which depicts a vinculariiform colony resembling *Filicea*, that it is not the same species as *E. dichotoma* sensu Reuss, 1874.

Canu (1897*b*) identified specimens here regarded as *Elea subhexagona* as *E. hexagona* d'Orbigny, a Santonian species which is very similar to *E. subhexagona* but which can be distinguished by the deep and prominent tubercle situated distally to the autozooidal aperture. Canu apparently realized later that this identification was mistaken because material of his in the MNHN and in the ZMC (donated to G.M.R. Levinsen) is labelled with the MS name '*Elea fissurata*'. The exact stratigraphical horizon of these specimens from St Calais (Sarthe) is questionable; Canu originally ascribed his St Calais material to the Cenomanian but subsequently referred it to the Turonian (Canu and Bassler, 1922). It seems possible that the specimens are from the late Cenomanian *plenus* Zone, although *E. subhexagona* is not represented among material of this age from St Calais in the VH and BMNH collections.

DISTRIBUTION. Upper Cenomanian/Lower Turonian of St Calais, Sarthe, France, and Upper Turonian of Dresden, Germany.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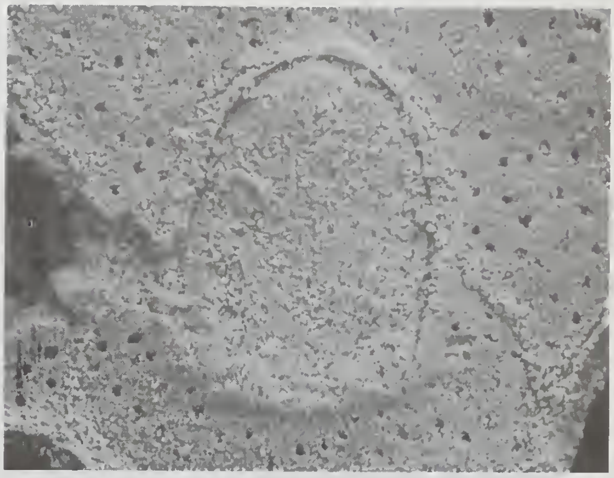
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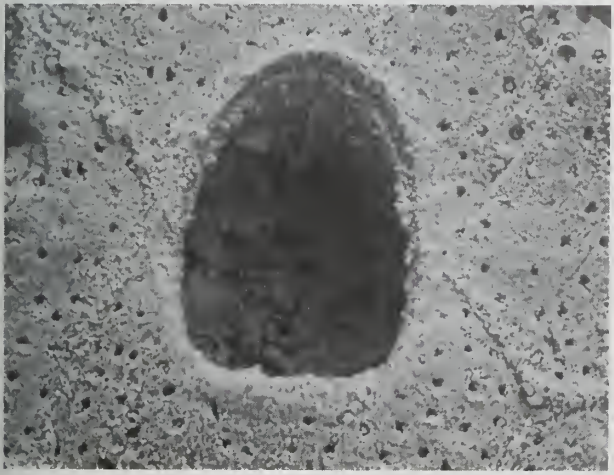
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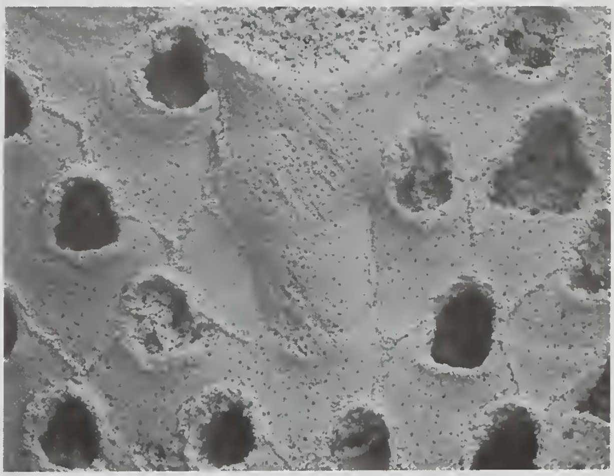
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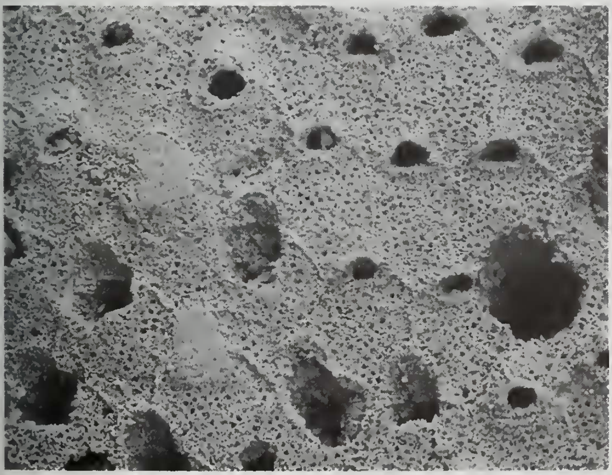
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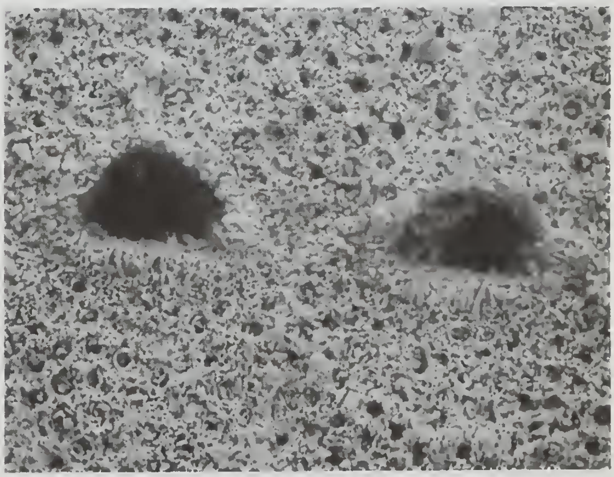
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Figs 72–77 *Elea pseudolamellosa* sp. nov. 72–74, VH 10461, Upper Campanian, St Severin d'Uzel, Charente Maritime, France; 72, autozooids and eleozooids (top left), × 47; 73, autozooidal operculum, × 250; 74, autozooidal aperture, × 250. 75, VH 10462, holotype, Upper Campanian, St Severin d'Uzel, gonozooid origin with kenozooid above and to the left of the maternal zooid, × 65; 76, 77, VH 10471, Senonian, Le gare de Soullans, Vendée, France; 76, eleozooids and autozooids, × 65; 77, apertures of two eleozooids, × 250.

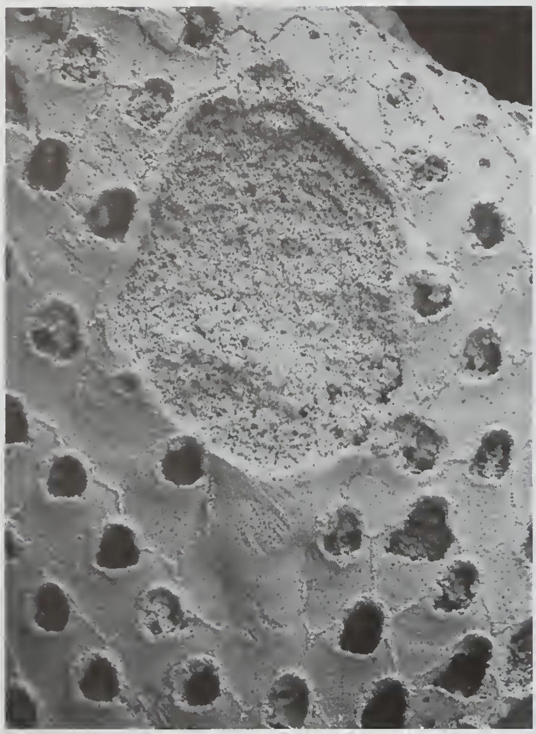

Fig. 78 *Elea pseudolamellosa* sp. nov., VH 10462, holotype, Upper Campanian, St Severin d'Uzel, Charente Maritime, France; gonozooid with broken roof, × 42.

Fig. 79 *Elea subhexagona* sp. nov., ZMC Levinsen Collection M54, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; branch with autozooids, eleozooids and distally, an overgrowth of kenozooids occupying the areas between zooidal apertures; × 39.

Elea triangularis (Michelin, 1841) Figs 87–94

1841 *Eschara triangularis* Michelin: 5, pl. 1, fig. 6.
1850 *Eschara triangularis* Michelin; d'Orbigny: 140.
1851 *Eschara triangularis* Michelin; d'Orbigny, pl. 602, figs 4 and 5.
1853 *Elea triangularis* (Michelin); d'Orbigny: 630, pl. 737, figs 17–20.
1890 *Elea triangularis* (Michelin); Pergens: 397.
1899 *Elea triangularis* (Michelin); Gregory: 305.
1975 *Elea triangularis* (Michelin); Walter: 314, pl. 29, figs 1, 5.

MATERIAL. Holotype: MNHN Michelin Collection un-numbered (Fig. 87), Albian, Grandpré, Ardennes, France. Other material: MNHN d'Orbigny Colln 6020 (5 pieces mounted on a tablet with the mark of a sixth, lost piece), same horizon and locality as holotype; BMNH 60541 (large colony and several fragments), 'Gault Chloritic' (probably Lower Albian *mammillatum* Zone according to H.G. Owen pers. comm.), Folkestone, Kent, UK; BMNH D52080 (SEM stub), Lower Albian (*tardefurcata* or *mammillatum* Zone, see Owen, 1972; Rawson *et al.*, 1978), Shenley Limestone, Leighton Buzzard, Bedfordshire, UK, R.J. Hogg Collection.

DESCRIPTION. Colony bifoliate (Fig. 87) with narrow, folded branches which bifurcate occasionally; branches generally 6 mm wide and 1 mm deep. Zooids arranged in approximate quincunx; organization fixed-walled. Colony base hollow (in holotype). Growing edge often arcuate. Overgrowths sometimes developed on erect branches. Zooidal buds may be occluded by terminal diaphragms located well proximal to the interzooidal wall ends.

Autozooids (Fig. 89) medium-sized, generally rhombic with relatively short, convex frontal walls pierced by large, circular, slightly countersunk pseudopores; zooidal boundaries raised. Apertures (Fig. 90) very large, elongate, almost 1·5 × longer than wide, attaining maximum width a little distal to the hinge line, well-rounded distally; apertural shelf present only in the mid-part of the aperture, indenting the margins of the aperture and producing the bell-shape typical of the species; hinge line with a pair of prominent hinge teeth. Apertural rim thick, continuous with variably extensive but low tubercles at the lateral corners of the frontal wall. Opercula (Fig. 88) occasionally preserved in-situ, proximal edge a little concave, surface slightly convex, fissured and with about 25 elongate pseudopores arranged in an irregular crescent; internally (Fig. 92), prominent, inward-sloping sclerites form a continuous arch immediately outward of the pseudopores. Intramurally budded autozooids may be present. A tubular structure apparently composed of

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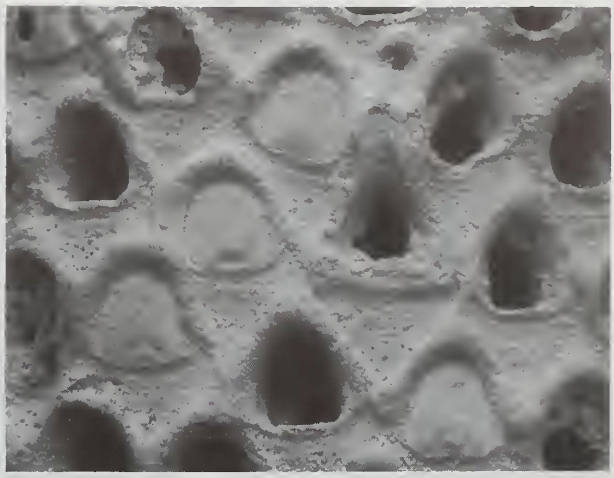

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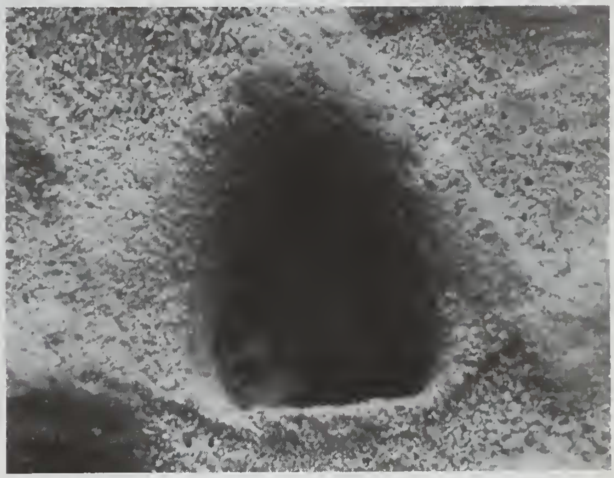

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Figs 80–83 *Elea subhexagona* sp. nov. 80, DM un-numbered, Voigt photocard 2060, holotype, Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany, autozooids, mostly with opercula, and eleozooids, × 45. 81–83, ZMC Levinsen Collection M54, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; 81, autozooids and a primary eleozooid containing an intramural eleozooid, × 70; 82, autozooidal operculum, × 210; 83, autozooidal aperture, × 210.

pseudoporous exterior wall, which can be seen within the aperture of one zooid (Fig. 91), is interpreted as a bioclaustration (i.e. an embedment structure formed by the bryozoan; cf. similar structures in Cretaceous onychocellids attributed to the presence of folliculinid protists by Ernst, 1985). Interzooidal walls with conspicuous pores. Mural spines present in great abundance in the proximal parts of zooids, long, and either simple or branched (Fig. 93).

Eleozooids unknown, presumed absent.

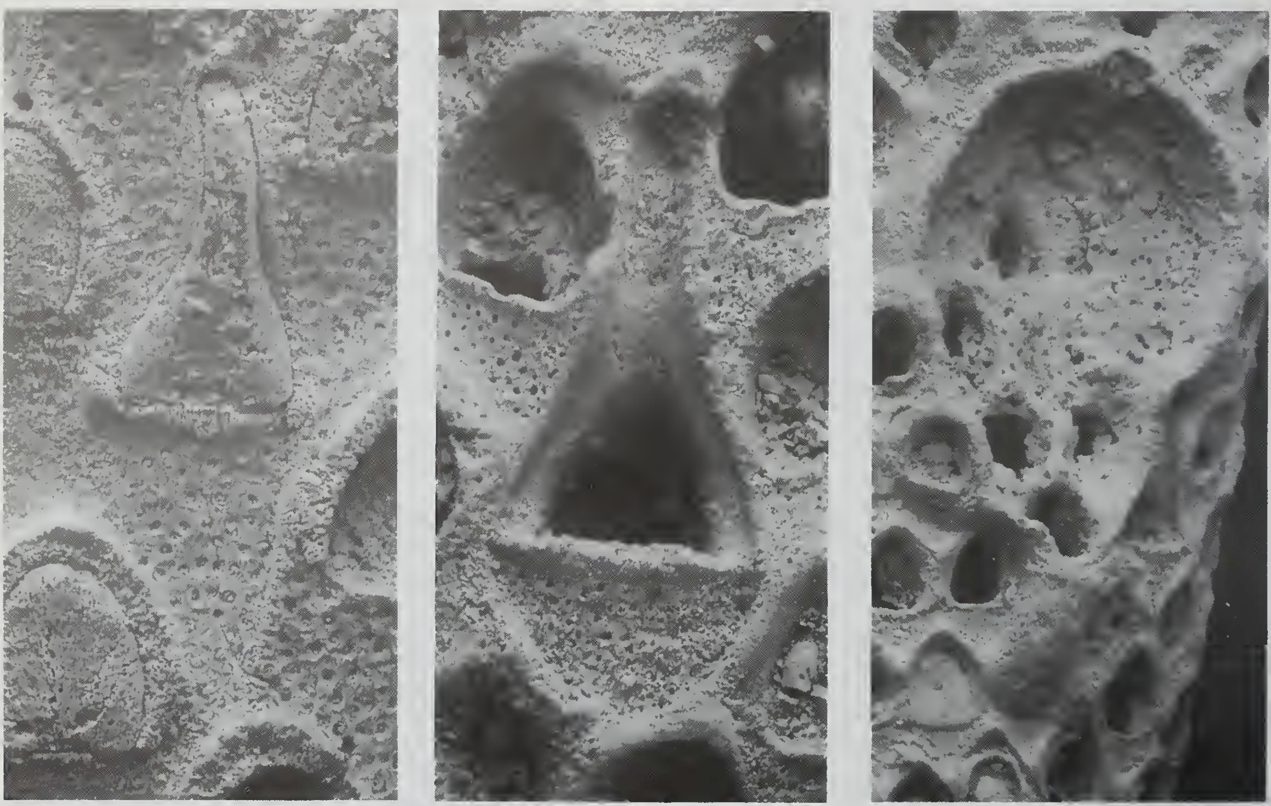
Kenozooids sometimes present.

Gonozooid known from only one partly developed example (Fig. 94) showing the tubular, densely pseudoporous proximal part of the frontal wall emerging from the aperture of the maternal zooid.

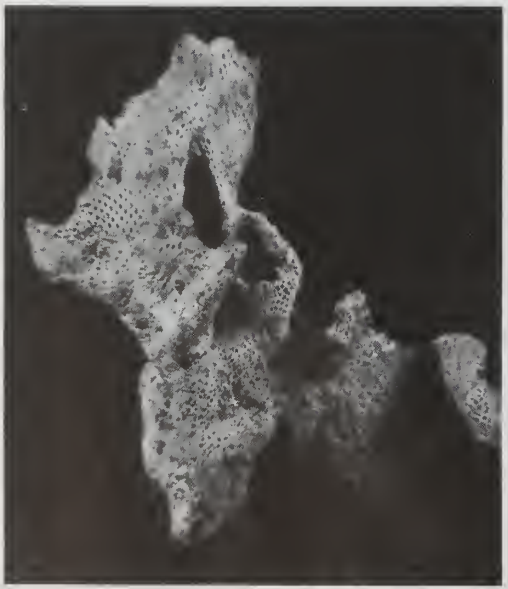
Measurements.
autozooids (10 zooids from BMNH 60531)
frontal length: mean = 0·55 mm; SD = 0·036 mm; CV = 6·6; range = 0·50–0·60 mm
frontal width: mean = 0·35 mm; SD = 0·027 mm; CV = 7·8; range = 0·32–0·39 mm
apertural length: mean = 0·29 mm; SD = 0·015 mm; CV = 5·2; range = 0·27–0·32 mm
apertural width: mean = 0·20 mm; SD = 0·011 mm; CV = 5·2; range = 0·20–0·23 mm

Remarks. The large size and characteristically bell-shaped autozooidal apertures immediately distinguish this uncommon species from others in the genus. *E. triangularis* is the only bifoliate melicerititid described from the Lower Cretaceous. It is also currently unique in being the only melicerititid known to possess mural spines (= zooecial or intrazooecial spines) (Fig. 93). Similar structures are, however, common and widely distributed taxonomically among non-melicerititid cyclostomes (see Farmer, 1979) and further investigations of the internal morphology of melicerititids will probably reveal more examples.

Distribution. Albian (?Lower Albian only) of France and England.



Figs 84–86 *Elea subhexagona* sp. nov. 84, DM un-numbered, Voigt photocard 2060, holotype, Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany, eleozooid with operculum, × 145. 85, 86, ZMC Levinsen Collection M53, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; 85, eleozooid, × 120; 86, damaged gonozooid, × 53.

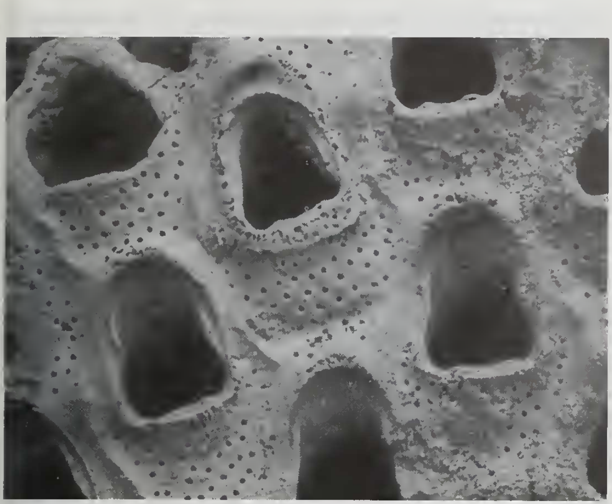


87

Fig. 87 *Elea triangularis* (Michelin, 1841), photograph of the holotype colony, MNHN Michelin Collection un-numbered, Albian, Grandpré, Ardennes, France; × 2·5.

88

Fig. 88 *Elea triangularis* (Michelin, 1841), BMNH D52080, Lower Albian (*tardefurcata* or *mammillatum* Zone), Shenley Limestone, Leighton Buzzard, Bedfordshire, UK; secondary electron image of coated specimen showing autozooidal operculum in slightly oblique view, × 117.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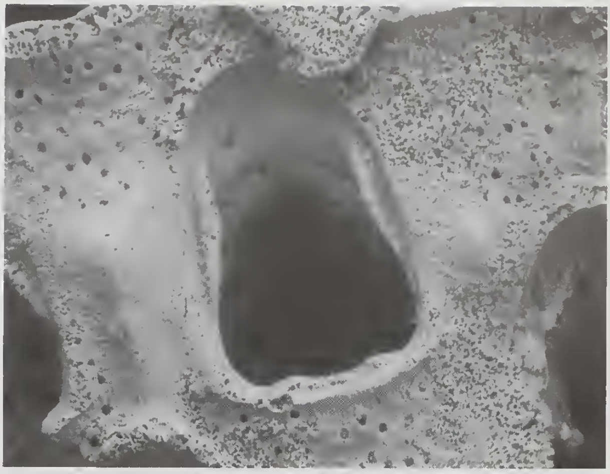
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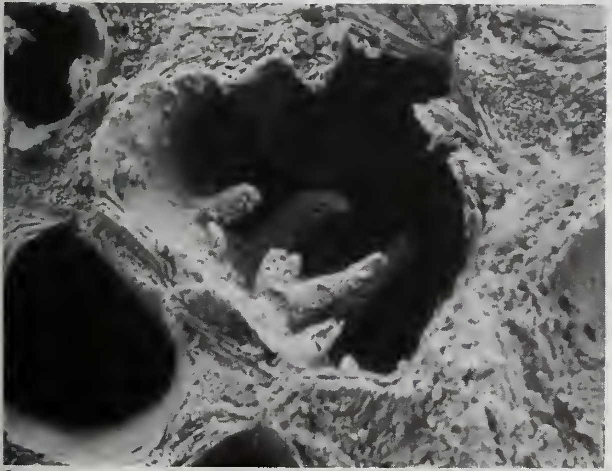
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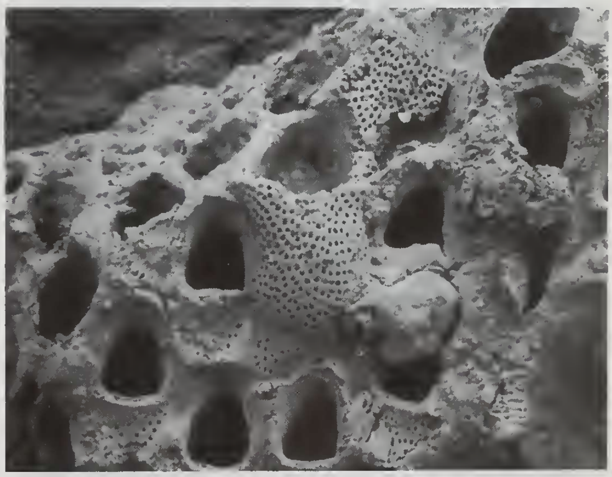
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Figs 89–94 *Elea triangularis* (Michelin, 1841), BMNH 60531, 'Gault Chloritic' [probably Lower Albian *mammillatum* Zone], Folkestone, Kent, UK; 89, group of autozooids, including one with an intramural autozooid (upper centre), × 62; 90, autozooidal aperture, × 125; 91, autozooidal aperture containing enigmatic tubular structure, × 120; 92, inner side of an autozooidal frontal wall and operculum showing sclerites and pseudopores, × 118; 93, fractured specimen exposing mural spines within the proximal chamber of an autozooid, × 355; 94, proximal part of a broken gonozooid, × 37.

Elea viskovae sp. nov. Figs 95–99

Material. Holotype: VH 10450, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection. Paratypes VH 10542 (6 specimens), details as for holotype.

Name. In honour of the Russian bryozoologist L.A. Viskova.

Description. Colony bifoliate with branches (Fig. 95) narrow, strap-like, bifurcating, about 1·3–2·0 mm wide and 0·5–0·6 mm deep. Autozooidal arrangement variable, both autozooids and eleozooids divergent close to branch margins; organization fixed-walled. Overgrowths common. Colony base unknown. One of the paratypes grows against and partially envelops a ?serpulid tube.

Autozooids (Fig. 96) large; frontal walls irregularly hexagonal, distally rounded, elongate, 2·5–3 × longer than wide, with circular pseudopores; zooecial boundaries raised. Apertures (Fig. 99) of moderate size, longitudinally elongate, on average 1·1 × longer than wide, attaining maximum width just proximal to mid-length, appreciably narrower at hinge line level, well-rounded distally; apertural shelf broad, 0·02–0·03 mm wide, causing the aperture to have the shape of a high isosceles triangle with rounded corners; apertural rim moderately prominent; hinge line bowed. Opercula (Fig. 97) often preserved in-situ, slightly convex, with about 16 pseudopores arranged in a cresent parallel to the distal/lateral margin. Terminal diaphragms (Fig. 97) positioned proximally to the apertural shelf, ?non-pseudoporous. Intramural buds not observed with certainty.

Eleozooids (Figs 95, 96) common, located close to branch margins, about 2–2·5 longer than wide, their frontal walls a little longer and significantly wider than those of the autozooids. Aperture elongate, attaining maximum width slightly distally to the hinge-line, well-rounded distally; apertural shelf not clearly developed but rostral shelf present. Opercula known from only one partial example in-situ, surface strongly convex at preserved edges. Intramural buds not observed.

Kenozooids commonly present at branch margins.

Gonozooids not observed.

Fig. 95 *Elea viskovae* sp. nov., VH 10450, holotype, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection; branch with autozooids and marginal eleozooids, × 37.

Measurements.

autozooids (10 zooids with in-situ opercula from holotype VH 10450)

frontal length: mean = 0·64 mm; SD = 0·070 mm; CV = 10·9; range = 0·54–0·77 mm
frontal width: mean = 0·24 mm; SD = 0·024 mm; CV = 9·6; range = 0·21–0·29 mm
apertural length: mean = 0·19 mm; SD = 0·009 mm; CV = 4·4; range = 0·18–0·21 mm
apertural width: mean = 0·17 mm; SD = 0·010 mm; CV = 6·0; range = 0·17–0·20 mm

eleozooids (5 zooids from holotype VH 10450)

frontal length: range = 0·63–0·80 mm
frontal width: range = 0·32–0·35 mm
apertural length: range = 0·27–0·30 mm
apertural width: range = 0·21–0·24 mm

Remarks. The marginal eleozooids of *Elea viskovae*, which resemble slightly-enlarged autozooids, distinguish this new species from others within the genus *Elea*. They have less well-developed rostra than those of *E. mackinneyi*, a species with smaller autozooids. Eleozooid morphology recalls that present in such species as *Meliceritites semiluna* and *Biforicula filicosa*.

Many of the autozooidal opercula (and some terminal diaphragms) in the holotype are pierced by small circular borings (Figs 96–97) like those described previously in other melicerititids (Taylor, 1982).

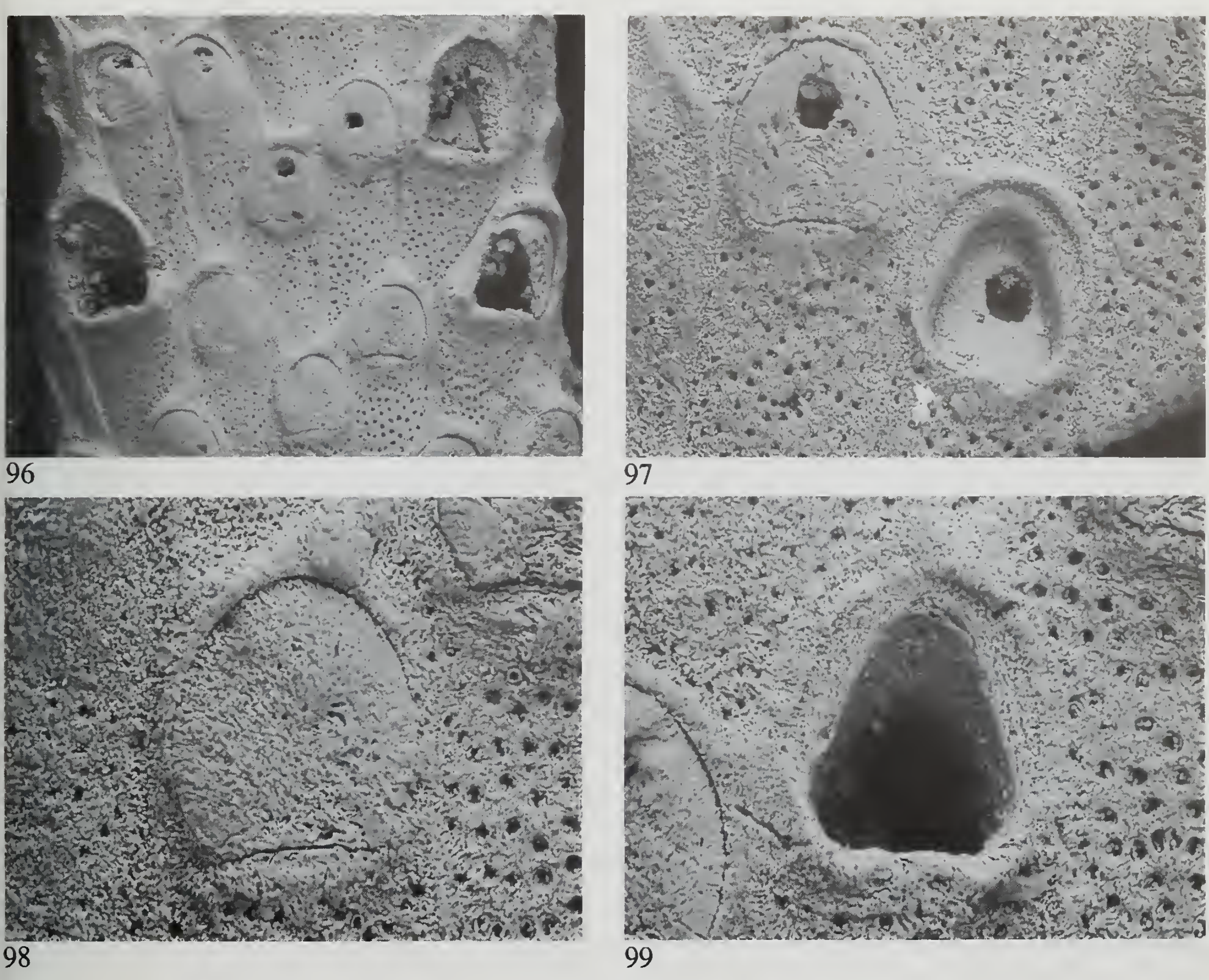
Distribution. Turonian of Kazakhstan.

Elea whiteleyi sp. nov. Figs 100–109

Material. Holotype: VH 10538, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France, collected by G. Breton 1981. Paratypes: VH 10439, 10539–40, same horizon and locality as holotype. BMNH D55027–8, Cenomanian [?Lower Cenomanian, Craie Glauconieuse], Bruneval, Seine-Maritime, France, S. Whiteley Collection. Other material: VH, numerous un-numbered topotypes.

Name. In honour of the late S. Whiteley, an enthusiastic amateur geologist who collected paratypes of this species.

Description. Colony bifoliate with bifurcating, narrow strap-like branches about 1·1–2·3 mm wide and 0·6 mm deep, elliptical in cross-section. Autozooids arranged more or less



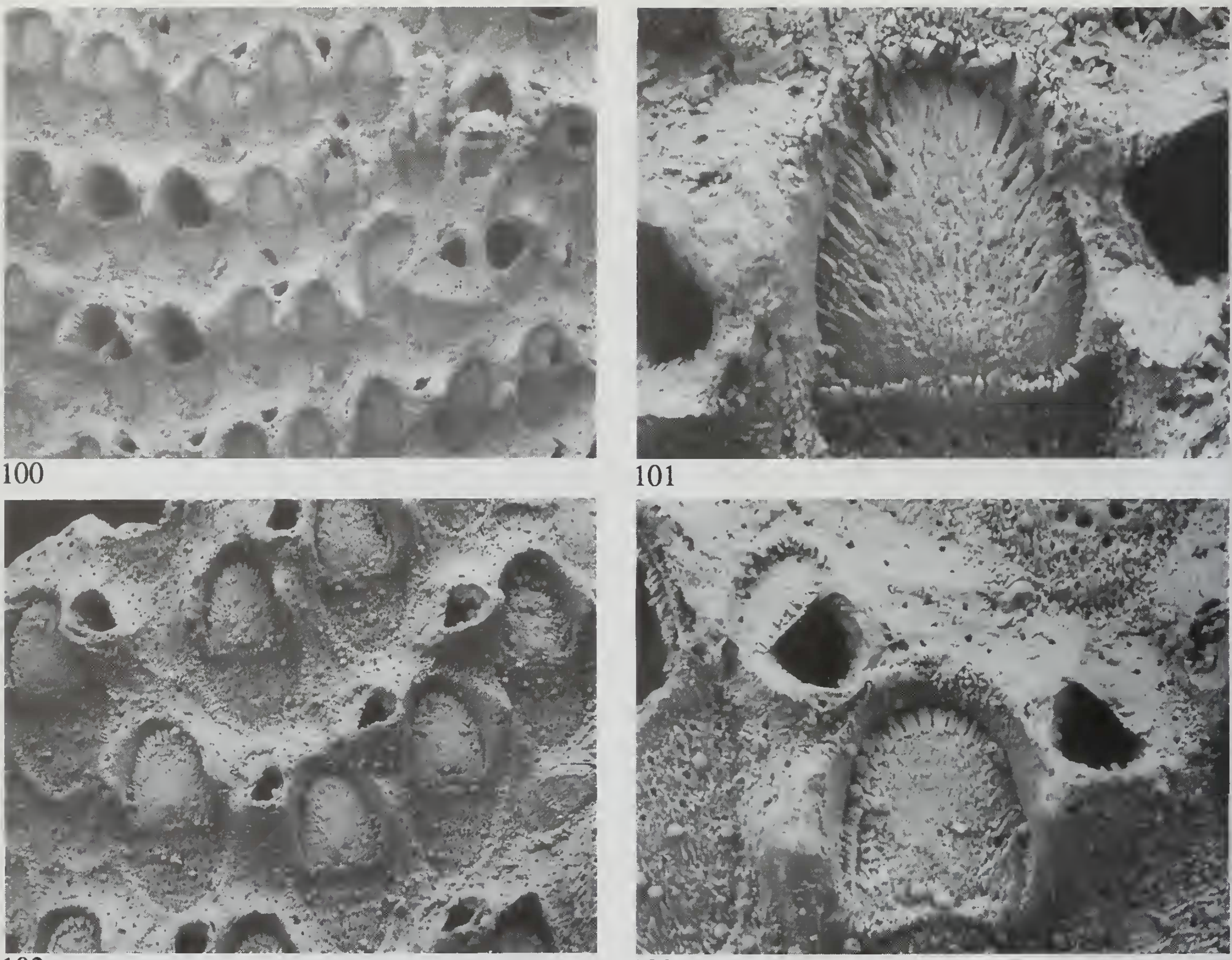
Figs 96–99 *Elea viskovae* sp. nov., VH 10450, holotype, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection; 96, autozooids with opercula, some bored, and three marginal eleozooids, × 62; 97, bored autozooidal operculum (upper left) and terminal diaphragm (lower right), × 160; 98, autozooidal operculum, × 250; 99, autozooidal aperture, × 250.

in quincunx or in ill-defined transverse rows (Fig. 100), separated from adjacent autozooids by demizooids; organization fixed-walled. Overgrowths moderately common, at least some formed by eruptive budding onto surfaces of erect branches, sometimes consisting predominantly of demizooids and kenozooids . Colony base (Figs 105–107) extensive, giving rise to several erect branches whose median budding laminae are parallel to local orientation of basal zooids; demizooids of base have higher, more pointed apertures than those of erect branches, and many possess non-inclined apertures orientated parallel to adjacent autozooids.

Autozooids (Figs 102, 104) small, with longitudinally elliptical pseudoporous frontal walls, about twice as long as wide, depressed with respect to the surrounding demizooids. Apertures small, longitudinally elongate, about 1·1 × longer than wide, attaining maximum width at a level between the hinge line and mid-length; apertural shelf slight; apertural rim prominent, sometimes prolonged at the mid-point of the aperture; hinge line with a curved median bar. Opercula (Fig. 101) very often preserved in-situ, surface moderately convex, a flattened median proximal area often evident, bearing an estimated 14–18 slit-shaped pseudopores in a crescent close to the lateral/distal edge. Intramural buds and terminal diaphragms not observed.

Rostrozooids (Figs 105, 108) moderately common, usually occurring singly close to the branch mid-line just before a bifurcation, but sometimes located close to branch margins, elongate, about 3–5 × longer than wide. Aperture long, attaining maximum width at the hinge line, very slightly spatulate, rounded distally, about 3–4 × longer than wide. In-situ opercula not seen. Rostrozooids and/or demizooids may be budded intramurally within rostrozooids (Fig. 108).

Demizooids (Fig. 103) numerous, normally about 2 per autozooid, often paired disto-laterally on either side of an autozooidal aperture; frontal walls usually long and narrow, forming raised areas between frontal walls of laterally adjacent autozooids, their boundaries, however, poorly-defined; apertures variously orientated, many in oblique or reverse orientation with respect to colony growth direction, typically in a plane inclined about 60° to the colony surface, small, semicircular to longitudinally elongate in shape, rounded or slightly arched distally. Opercula often preserved in-situ; terminal diaphragms observed.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Figs 100–103 *Elea whiteleyi* sp. nov., top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France. 100–101, VH 10539; 100, branch surface, × 53; 101, autozooidal operculum, × 330. 102, 103, VH 10538, holotype; 102, autozooids, kenozooids, and demizooids with obliquely-directed, inclined apertures, × 95; 103, operculate autozooid and two demizooids, × 220.

Kenozooids (Figs 102, 105) observed commonly in colony base, overgrowths, and at the margins of erect branches.

Gonozooids (Fig. 109) fairly common. Distal frontal wall emerging from maternal aperture initially parallel-sided before becoming bulbous and longitudinally ovoidal in shape. Ooeciopore located beyond inflated part of frontal wall, transversely elliptical, about 1·5 × wider than long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10538)

frontal length:	mean = 0·33 mm; SD = 0·015 mm; CV = 4·5; range = 0·30–0·35 mm
frontal width:	mean = 0·17 mm; SD = 0·008 mm; CV = 4·5; range = 0·17–0·18 mm
apertural length:	mean = 0·15 mm; SD = 0·005 mm; CV = 3·1; range = 0·15–0·17 mm
apertural width:	mean = 0·13 mm; SD = 0·006 mm; CV = 4·8; range = 0·12–0·14 mm

rostrozooids (5 zooids from 5 colonies)

frontal wall length:	range = 0·63–0·92 mm
frontal wall width:	range = 0·20–0·21 mm
apertural length:	range = 0·33–0·57 mm
apertural width:	range = 0·11–0·15 mm

demizooids

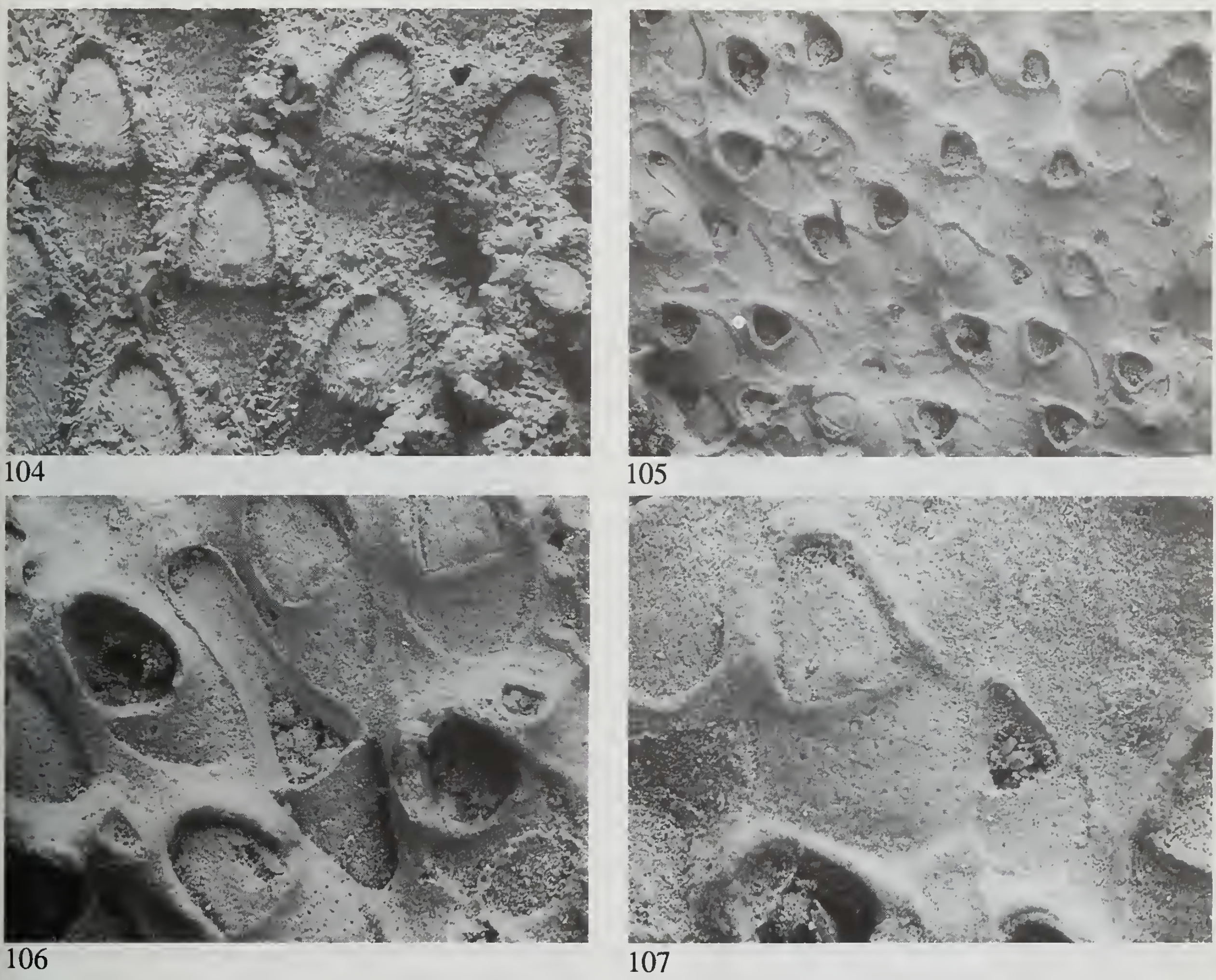
apertural width:	*ca* 0·06–0·09 mm

gonozooids (one zooid from holotype VH 10538)

total frontal wall length:	2·36 mm
dilated frontal wall length*:	1·13 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·12 mm

(* i.e. that part of the frontal wall distal to the narrow origin)

REMARKS. The presence of numerous small eleozooids enables this new species to be readily distinguished from all other species of *Elea*, including *E. elegantula* which it most



Figs 104–107 *Elea whiteleyi* sp. nov. 104, BMNH D55027 Cenomanian [?Lower Cenomanian, Craie Glauconieuse], Bruneval, Seine-Maritime, France, operculate autozooids (demizooids obscured by diagenetic cement), × 98. 105–107, VH 10439, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France; encrusting colony base; 105, irregular arrangement of autozooids, kenozooids, small eleozooids and a large eleozooid, × 40; 106, large eleozooid (rostrozooid), × 100; 107, operculate autozooid and small eleozooid, × 135.

resembles in the morphology of the other polymorphs. These eleozooids and their distribution surrounding the autozooids invite comparison between *E. whiteleyi* and the Upper Cenomanian bifoliate melicerititid *Biforicula multicincta*, the oldest known species of *Biforicula* (see Voigt, 1989) The principal qualitative difference between *E. whiteleyi* and *B. multicincta* is the existence of cancelli in the latter. It therefore seems possible that *E. whiteleyi* belongs in the stem-group of *Biforicula*.

DISTRIBUTION. Lower-Middle Cenomanian of Normandy, France.

Genus *SEMIELEA* d'Orbigny, 1853

TYPE SPECIES. *Entalophora vieilbanci* d'Orbigny, 1850, designated by Bassler (1935: p. 198) as '*S. vielbanci* D'Orbigny, 1853' [sic].

OTHER SPECIES. *Semielea dichotoma* d'Orbigny, 1853.

REVISED DIAGNOSIS. Eleid with tubular colony-form; axial lumen of subequal diameter lined by an inferred exterior wall; zooids in primary layer orientated parallel to tube length; autozooids fixed-walled; cancelli lacking.

REMARKS. D'Orbigny (1853) referred three species to *Semielea*. Only the first two are here retained in the genus; the third, *Semielea plana* d'Orbigny, 1853 is regarded as the base of *Elea lamellosa* (d'Orbigny, 1850) (see p. 19).

Diagnostic of *Semielea* is the possession of branches with an axial lumen, the bounding wall of which forms a lamina for zooidal budding. The axial lumen is intermediate in size between the narrow axial canals present in some species of *Meliceritites* (e.g. *M. semiclausa* (Michelin)) and the wide tubular interiors of certain specimens of *Reptomultelea* with cavariiform colonies. The growth of the axial lumen in *Semielea* also seems distinct. Although no specimens have

Fig. 108 *Elea whiteleyi* sp. nov., VH 10539, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France; primary rostrozooid containing intramural rostrozooid in turn containing intramural demizooid, × 120.

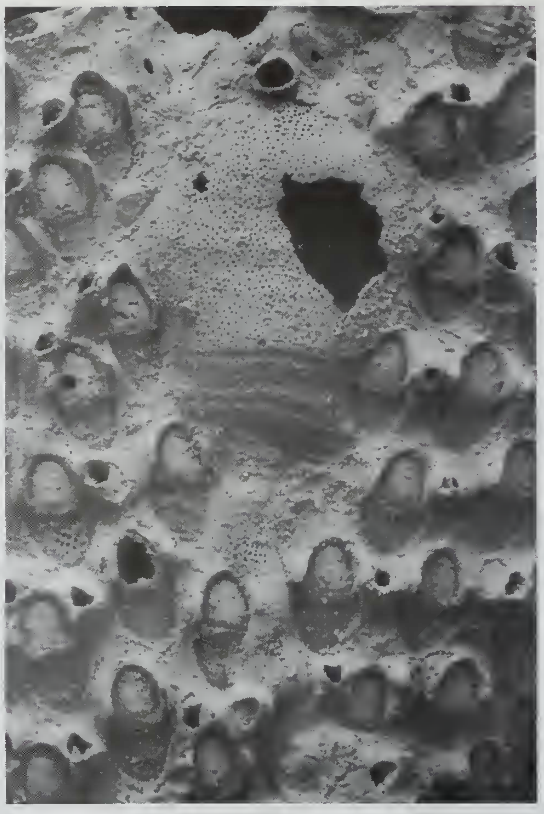


Fig. 109 *Elea whiteleyi* sp. nov., VH 10538, holotype, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France; gonozooid, × 50.

been studied with their microstructure sufficiently well-preserved to prove that the wall which lines the lumen is an exterior wall rather than an interior wall, the transverse folding and wrinkling of this wall (Fig. 119) strongly suggests that it is an exterior wall. Rare examples of colony bases viewed from the underside (Fig. 122) show that the lumen of each branch opens at the colony base and that the lumen wall is smoothly continuous with the basal lamina. As the basal lamina is an undoubted exterior wall, this observation is further evidence that the lumen walls are exterior. In *S. vieilbanci* occasional transverse platforms partition the axial lumen and seem to have been formed by progressive constriction of the lumen. The presence of these platforms, which would have periodically sealed the entrance to the lumen at branch growth tips, may explain why fouling of the apparent exterior walls lining the lumen has not been observed (cf. exterior walls lining the tubes of cavariiform *Reptomultelea* colonies). The platforms also imply that branches could not have grown around another erect organism (cf. some species of *Reptomultelea*), but instead grew freely into space.

The phylogenetic relationship is unclear between *Semielea* and species of *Meliceritites* on the one hand and of *Reptomultelea* on the other. Assuming *Semielea* to be a relatively advanced genus, it could have derived from either of the two latter genera. Derivation from *Meliceritites* would necessitate the incorporation of tubular prolongations of the basal lamina into the centre of the erect cylindrical branches, together with loss of the normal endozonal budding pattern. Derivation from *Reptomultelea* would require formation of tubular prolongations of the basal lamina to give erect cylindrical branches. On the grounds of parsimony, the latter alternative seems the more likely, but future phylogenetic analysis, including zooid-level characters, might provide better evidence of affinity.

DISTRIBUTION. Turonian (?Upper) – Lower Santonian, northern France.

Semielea vieilbanci (d'Orbigny, 1850) Figs 110–122

1850 *Entalophora vieilbanci* d'Orbigny: 200.
1851 *Diastopora vieilbanci* (d'Orbigny); d'Orbigny, pl. 637, figs 7–8.
1851 *Diastopora arborescens* d'Orbigny: pl. 638, figs 1–5.
1853 *Semielea vieilbanci* (d'Orbigny); d'Orbigny: 636, pl. 738, figs 5–9.
1853 *Semimultelea arborescens* (d'Orbigny); d'Orbigny: 652, pl. 741, fig. 5.
1890 *Semielea vieilbanci* (d'Orbigny); Pergens: 392.
1893 *Semielea vieilbanci* (d'Orbigny); Pergens: 211.
?1897*a* *Semielea vieilbanci* (d'Orbigny); Canu: 155.
?1897*b* *Semielea vieilbanci* (d'Orbigny); Canu: 750.
1899 *Elea vieilbanci* (d'Orbigny); Gregory: 300, fig. 33.

Fig. 110 *Semielea vieilbanci* (d'Orbigny, 1850), photograph of MNHN d'Orbigny Collection 6965 (part), Turonian, France; × 8·5.

1912 *Meliceritites vieilbanci* (d'Orbigny); Levinsen: 47, pl. 1, figs 15 and 16.
1953 *Semielea vielbanci* [sic] (d'Orbigny); Bassler: G77, fig. 40, 3a, b.
1981 *Semielea vieilbanci* (d'Orbigny); Voigt: 453, fig. 5a.

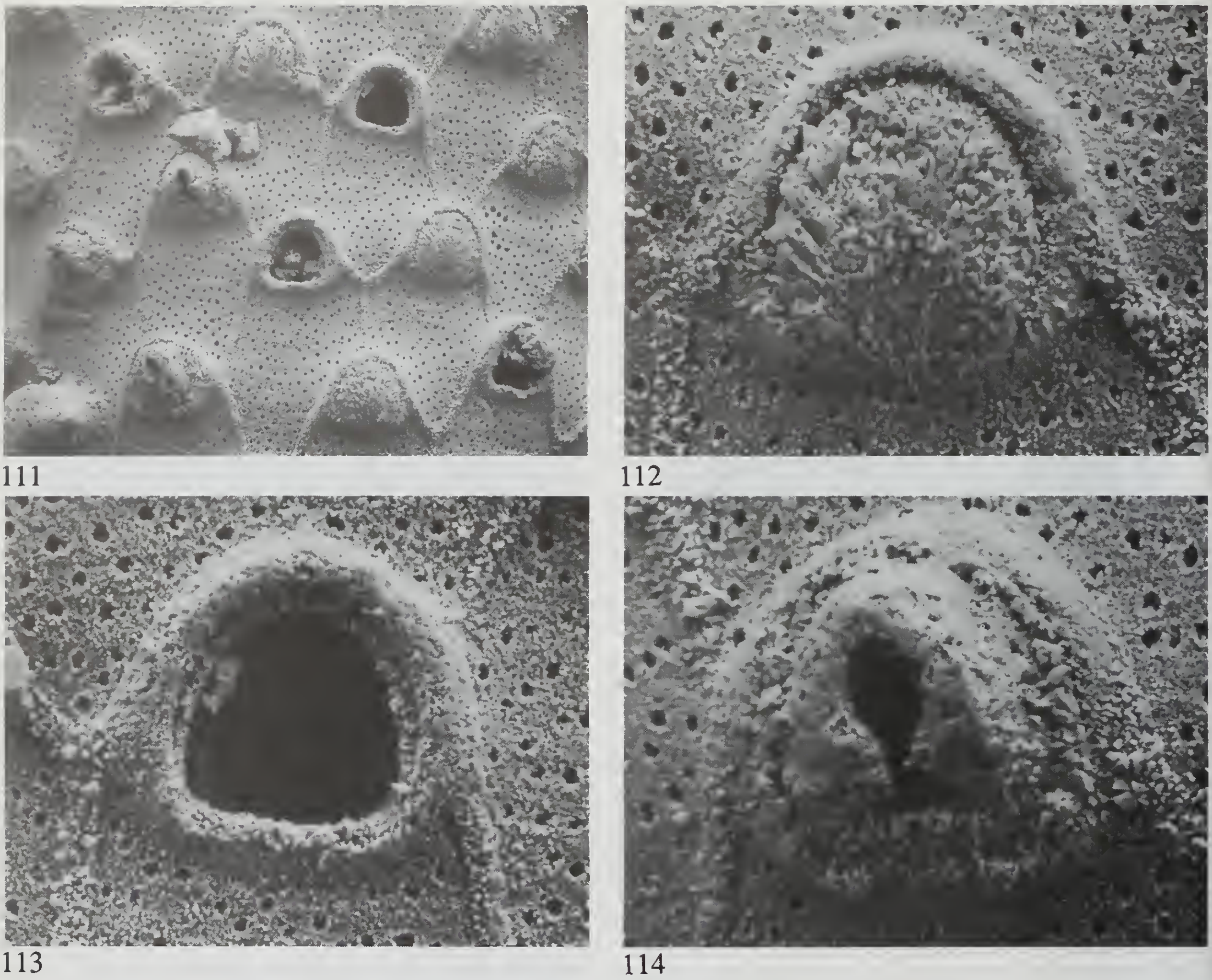
MATERIAL. Type: there is no material of this species from the type locality (Turonian of Tourtenay; see d'Orbigny 1850, p. 200) in the d'Orbigny Collection, MNHN, although over a hundred specimens from the Turonian of several other localities are registered under number 6965 (e.g. Fig. 110). In view of the absence of topotype specimens, together with the unequivocal identity of the species, no neotype designation is made.

Other material: MNHN d'Orbigny Colln 6965, over 100 pieces from the Turonian of various localities in France, including Troot, St Maure, Tours, Angouleme, Villavard. MNHN d'Orbigny Colln 8200 (Figs 121, 122), Senonian, ?Villedieu, ?Vendôme, syntypes of *Diastopora arborescens* d'Orbigny, 1851, several specimens including Voigt Photocard 8312 and an un-numbered specimen corresponding to that illustrated by d'Orbigny (1851: pl. 638, fig. 2). ZMC Levinsen Colln unnumbered, Bruillé Poncé and Villedieu, France. VH unnumbered: U. Turonian, Souge; Turonian, Les Ulmes, Eure; U. Turonian, Bois de Gareau, nr Ecommoi, Sarthe; U. Turonian, Angoumien, La Charte sur la Loire; U. Turonian, Sougé, Loir-et-Cher; Turonian, Luynes, Indre et Loire; Turonian, Les Ulmes, Maine; U. Turonian, Troot, Loir-et-Cher; U. Turonian, Les Roches, Loir-et-Cher; Turonian, Les Ulmes, Maine; U. Turonian/Coniacian, La Barre, nr St Maure, Indre et Loire; Coniacian, St Paterne, Indre et Loire; Coniacian, Tours, Indre et Loire; Coniacian, Fécamp, Seine Maritime. BMNH D3747 (4), 'Senonian', Lavardin, Gamble Colln; D8959–60, 'Senonian', Lavardin; D4807, Craie de Villedieu [Coniacian or Santonian], S. of les Roches; D4673, Craie de Villedieu, Luynes; D4679, D4800, D4806, D4860 (4), [Turonian], Montloire; D4675, D4676 (5), D4677, D4678 (4), D4683 (6), D4684 (3), D4715, D4799, D4811 (2), D4839, D4840 (3), D4861, D4862 (5), D4864 (2), D4865, D4868, D13573, Craie Marneuse, Villardin; D4937, [?Turonian], 'Nodula Chalk', Villardin Castle, purchd F.H. Butler; D4674 (figd Gregory, 1899: fig. 33), D4685, Craie Marneuse, Chinon; D33939–40, Turonian, St Calais, Sarthe, E. Darteville Colln; D36151–5, 'Senonian', Lavardin, Loir-et-Cher, Pergens Colln; D36156, Turonian, Lavardin, Loir-et-Cher, Pergens Colln; D53444, Turonian, Les Ulmes, Maine, Voigt Colln; D59368, Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 20 of Jarvis *et al.* (1982), La Bouchardière, Villedieu, Loir-et-Cher; D59369 (3), Craie de Villedieu [Coniacian or Santonian], Luynes; D59370–2, D59373 (3), D59374 (6), D59375 (sample), Turonian, Lavardin, Loir-et-Cher, F. Canu Colln; D59376 (6), Turonian, Châtellerault, Vienne, France; BZ 729 (sample), Turonian, St Maure, Indre-et-Loire, France, presd E. Voigt, November 1991.

DESCRIPTION. Colony tubular (cavariiform) with branches (Fig. 110) bifurcating, normally subcircular in cross-section but becoming elliptical immediately prior to bifurcation, varying from about 1·0 to 4·4 mm in diameter, typically 3·5–4·5 mm. Axial lumen lined by transversely wrinkled, inferred exterior wall (Fig. 119) and generally 0·6–1·4 mm in minimum diameter, becoming elliptical in cross section prior to dividing at branch bifurcations. Single layer thickness about 0·3–0·5 mm. Budding apparently occurs only on the lumen-lining wall. Overgrowths occasionally present, originating through intrazooecial fission, either disc-shaped and multidirectional or fan-shaped and unidirectional (Fig. 118); pseudoancestrula an autozooid, aperture about 0·09 mm long by 0·08 mm wide, initiating a secondary zone of astogenetic change of increasing zooid size. Zooid apertures arranged in rough quincunx or in rows transverse to growth direction. Organization fixed-walled.

Autozooids (Figs 111, 115) of moderate size, frontally elongate, subhexagonal or subrhomboidal in outline, on average 1·7–1·8 × longer than wide, well-rounded distally; boundary wall salient, forming a widened wall with contiguous apertural rim at distal end of zooid; frontal wall flat proximally, sometimes slightly convex distally, pseudopores subcircular. Apertures (Fig. 113) small, occupying less than a third of the frontal area, approximately equidimensional or a little wider than long, attaining maximum width about mid-length, well-rounded distally; apertural rim salient; apertural shelf of moderate width, tapering proximally; hinge line poorly preserved in all scanned specimens, bowed. Opercula (Fig. 112) often preserved in-situ, convex, prominent; pseudopores radially elongate, numbering about 16, arranged in a crescent. Terminal diaphragms (Fig. 117) common, located just proximally to the apertural shelf, with a central depression and pore. Intramurally budded autozooids not observed. Intramurally budded eleozooids (Fig. 111) very common; aperture (Fig. 114) trifoliate, prominent.

Kenozooids (Fig. 116) uncommon, developed close to branch bifurcations.



Figs 111–114 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D59370, Turonian, Lavardin, Loir-et-Cher, France; 111, group of autozooids, some containing intramural eleozooids, × 75; 112, autozooidal operculum, × 330; 113, autozooidal aperture, × 330; 114, intramural eleozooidal aperture, × 365.

Eleozooids (Fig. 116) rare (excluding intramurally budded examples); frontally about the same length but narrower than the autozooids, pointed distally; aperture trifoliate; opercula not observed.

Gonozooids (Fig. 120) rare; frontally elongate, about twice as long as wide, the inflated frontal wall emerging from the maternal aperture initially parallel-sided, becoming longitudinally ovoidal distally. Ooeciopore and atrial ring not seen in poorly preserved specimens available for study.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from BMNH D59370)

frontal length:	mean = 0·47 mm; SD = 0·030 mm; CV = 6·4; range = 0·42–0·53 mm
frontal width:	mean = 0·27 mm; SD = 0·019 mm; CV = 6·9; range = 0·26–0·30 mm
apertural length:	mean = 0·13 mm; SD = 0·007 mm; CV = 5·5; range = 0·12–0·14 mm
apertural width:	mean = 0·14 mm; SD = 0·009 mm; CV = 6·3; range = 0·12–0·15 mm

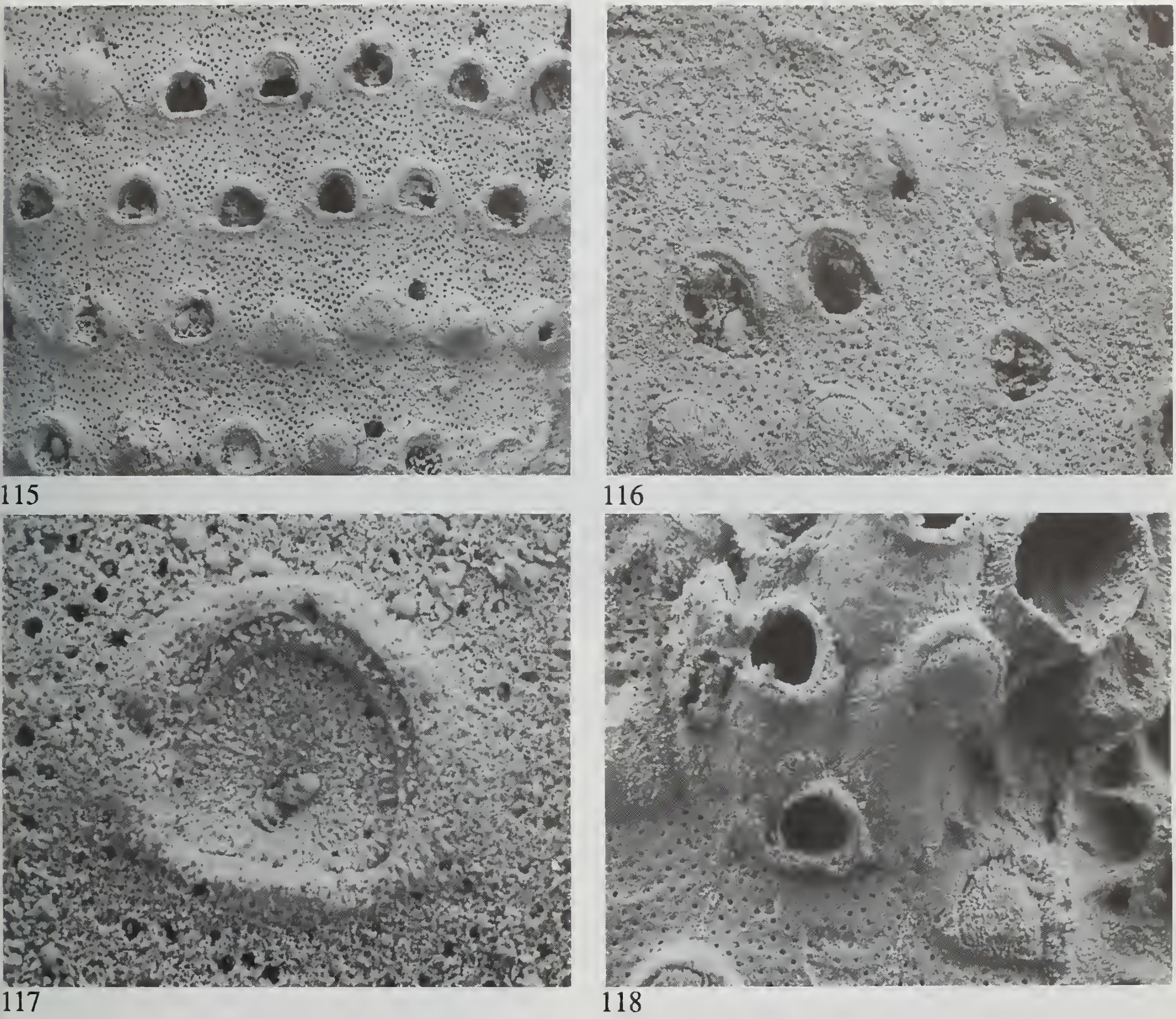
eleozooids (1 zooid from BMNH D36151)

frontal length:	0·48 mm
frontal width:	0·20 mm
apertural length:	0·09 mm
apertural width:	0·04 mm

gonozooids (2 zooids from BMNH D4674)

total frontal length:	1·86–1·91 mm
dilated frontal wall length:	1·56–1·65 mm
frontal width:	0·90–0·98 mm

REMARKS. This is a very common species. Most specimens come from the Upper Turonian of the Loire region of France, but the species ranges upwards into the Coniacian and evidently even into the basal Santonian. The wide axial lumen immediately distinguishes *S. vieilbanci* from similarly dendroid species of *Meliceritites* which, at most, only have narrow axial canals a little wider than the zooecial chambers. The small size of the apertures, particularly in comparison with frontal wall dimensions, distinguishes *S. vieilbanci* from



Figs 115–118 *Semielea vieilbanci* (d'Orbigny, 1850). 115–117, BMNH D36151, 'Senonian', Lavardin, Loir-et-Cher, France; 115, autozooids arranged in transverse rows, × 60; 116, autozooids, kenozooids and an eleozooid (centre) close to a branch bifurcation, × 100; 117, autozooidal aperture with terminal diaphragm, × 340. 118, BMNH D59371, Turonian, Lavardin, overgrowth origin, × 135.

S. dichotoma, and both species of *Semielea* differ from cavariiform colonies of *Reptomultelea* spp. in the consistently parallel orientation of the long axes of the zooids and the tubular branches.

DISTRIBUTION. Turonian (?Upper) – Lower Santonian, northern France.

Semielea dichotoma (d'Orbigny, 1851) Figs 123, 124

1851 *Diastopora dichotoma* d'Orbigny: pl. 638, figs 6–8.
1853 *Semielea dichotoma* (d'Orbigny); d'Orbigny: 637.
1890 *Semielea dichotoma* (d'Orbigny); Pergens: 393.
1912 *Meliceritites dichotoma* (?) (d'Orbigny); Levinsen: 38, pl. 5, figs 1 and 2.

MATERIAL. Lectotype: MNHN d'Orbigny Collection 8194 (Figs 123–124), specimen labelled as 'type' by E. Voigt, Voigt Photocard No. 8321, Senonian [?Coniacian], Tours, Indre et Loire, France. This specimen, a fragment 21 mm long which resembles but does not exactly match plate 638, figure 6 of d'Orbigny (1851), is one of several specimens of various species contained in six tubes and registered as 8194. No other material is available for study. E. Voigt (in litt. April 1984) states that 'Although I have got much material from Tours, I have never found this species in the French Turonian'.

DESCRIPTION. Colony tubular (cavariiform) with bifurcating branches (Fig. 123) about 2–3 mm in diameter. Overgrowths not observed. Organization fixed-walled. Zooid apertures variously arranged, often irregular.

Autozooids (Fig. 124) with short frontal walls. Apertures large, frontally elongate or equidimensional, closely-spaced, well-rounded distally; apertural rims thick and protruberant, especially distally; apertural shelf broad. Opercula often preserved in-situ, strongly convex and prominent. Terminal

Fig. 119 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D59372, Turonian, Lavardin, Loir-et-Cher, France; longitudinally fractured branch showing axial lumen with wrinkled lining wall, × 21.

diaphragms with a transverse depression present in many zooids. Intramurally budded eleozooids present; aperture triangular in shape, longer than wide.

Kenozooids not observed.

Eleozooids (except intramural buds) of uncertain presence.

Gonozooids not observed.

Measurements (approximate determinations taken from the lectotype MNHN d'Orbigny Collection 8194, Voigt Photocard 8321).

autozooids
apertural length: *ca* 0·21–0·25 mm
apertural width: *ca* 0·20–0·22 mm

eleozooids (probably intramurally budded)
apertural length: *ca* 0·17 mm
apertural width: *ca* 0·13 mm

Remarks. The description given above is based on examination of the lectotype using an optical microscope during a visit to the MNHN in 1985. Unfortunately, the species has not been studied using SEM and therefore detailed morphological information is lacking (type specimens from the d'Orbigny Collection, regrettably and much to the detriment of scientific knowledge, are not available for loan).

Semielea dichotoma differs from *S. vieilbanci* in having larger and more prominent autozooidal apertures which occupy a high proportion of the zooidal frontal surface, and intramurally budded eleozooids with triangular apertures.

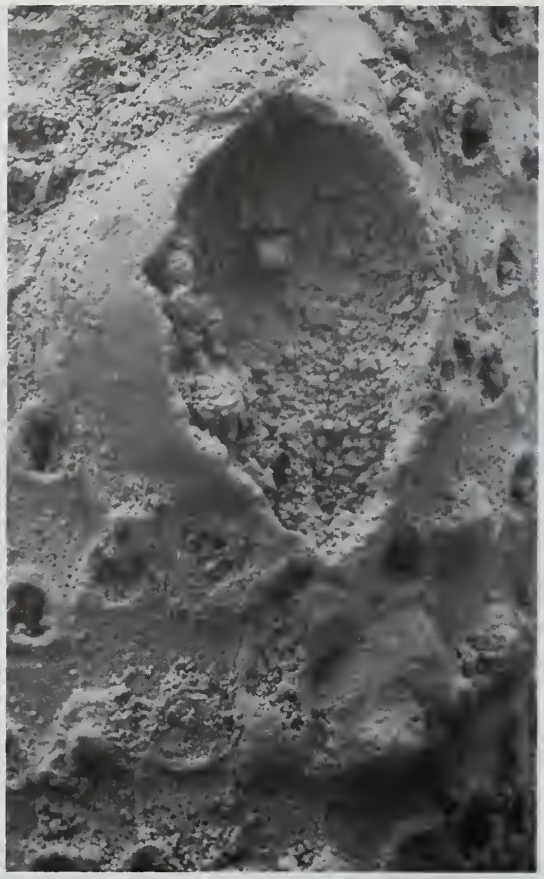


Fig. 120 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D4674, Craie Marneuse, Chinon, France; gonozooid with broken frontal wall and sediment-obscured ooeciopore, × 53.

Distribution. Senonian (?Turonian) of the Loire Region, France.

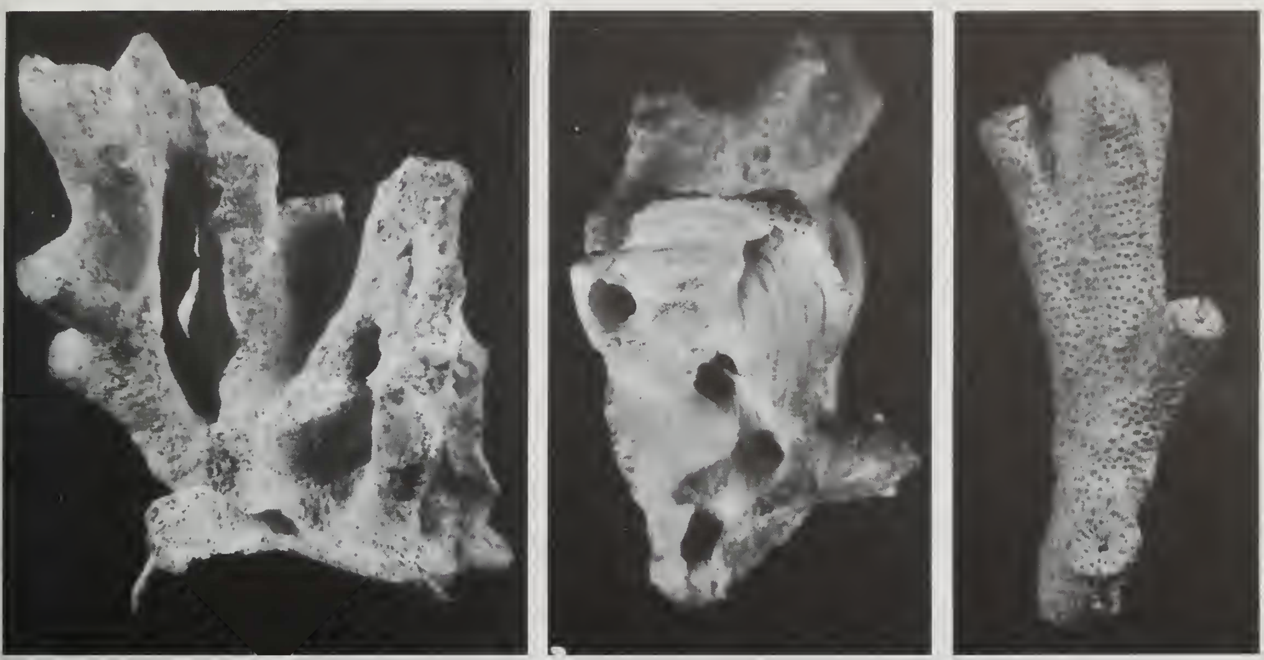
Genus *REPTOMULTELEA* d'Orbigny, 1853

Type species. *Reptomultelea tuberosa* d'Orbigny, 1853: p. 655, by monotypy, subjective junior synonym of *Reptelea sarthacensis* d'Orbigny, 1853: p. 640.

Other species. *Reptomultelea acclivata* sp. nov., *R. auris* sp. nov., *R. betusora* nom. nov. (for *Diastopora tuberosa* Reuss, 1874), *R. bituberosa* sp. nov., *Semimultelea canui* Voigt, 1924, *R. convexa* sp. nov., *S. dixoni* Lang, 1906, *Meliceritites filiozati* Levinsen, 1912, *R. goldfussi* sp. nov., *R. levinseni* sp. nov., *R. matutina* sp. nov., *R. mitrus* sp. nov., *Diastopora oceani* d'Orbigny, 1850, *R. parvula* sp. nov., *R. pegma* sp. nov., *Semimultelea polytaxis* Voigt, 1924, *R. pseudopalpebrosa* sp. nov., *R. reedi* sp. nov., *Semielea reussi* Pergens, 1890, *R. sarissata* Gregory, 1899, *R. scanica* sp. nov., *Clausimultelea tuberculata* d'Orbigny, 1853.

Revised diagnosis. Eleid with encrusting, unilamellar or multilamellar colony; autozooids fixed-walled; cancelli lacking.

Remarks. *Reptomultelea* is employed for a broad grouping of 23 fixed-walled melicerititids with non-erect, unilamellar



Figs 121–123 *Semielea* spp., photographs. 121–122, *S. vieilbanci* (d'Orbigny, 1850), MNHN d'Orbigny Collection 8200, Senonian, ?Villedieu, ?Vendôme, syntype of *Diastopora arborescens* d'Orbigny, 1851; 121, profile of colony with intact base; 3·2; 122, underside of base showing entrances to the axial lumens of four branches, × 4·1. 123, *S. dichotoma* (d'Orbigny, 1853), MNHN d'Orbigny Collection 8194, lectotype, Senonian [?Coniacian], Tours, Indre et Loire, France, × 3·7.

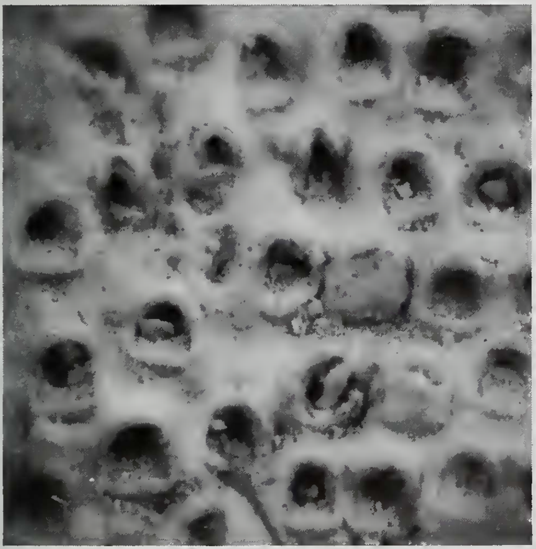


Fig. 124 *Semielea dichotoma* (d'Orbigny, 1853), photograph of MNHN d'Orbigny Collection 8194, lectotype, Senonian [?Coniacian], Tours, Indre et Loire, France; autozooids (some with opercula) and eleozooids (?intramural), × 38.

or, more often, multilamellar colonies. The oldest known species is *R. matutina* sp. nov. from the Lower Albian Shenley Limestone of Bedfordshire, England, and the youngest is *R. scanica* sp. nov. from the Lower Campanian of Scania, Sweden. Considerably more species (12) are recorded from the Cenomanian than from any other stage (see Fig. 127).

Table 4 is a key to species identification and should be used in conjunction with Figures 125 and 126 which depict the outline shapes of autozooidal and eleozooidal apertures. The species of *Reptomultelea* are fairly easy to separate if the material available is sufficient to access the character states of the autozooids and eleozooids. Variation between the small number of specimens available is relatively large for three of the new species (*R. convexa*, *R. goldfussi* and *R. mitrus*) recognized here. It is possible that one or more of these species will eventually require taxonomic splitting when further specimens become available.

Species of *Reptomultelea* are generally easily distinguished from the encrusting bases of erect melicerititids because of their large areal extent, typically multilamellar growth, regularity and generally high proportion of autozooids relative to eleozooids and kenozooids. Among species founded for non-erect colonies of melicerititids, *Reptoceritites rowei* Gregory, 1899 and *Reptoceritites acutissima* Voigt, 1963 fail to meet these criteria and are considered to be the encrusting bases of colonies of *Meliceritites* rather than species of *Reptomultelea*.

A difficult problem concerns the phylogenetic relationships between species of *Reptomultelea* and species of erect fixed-walled melicerititids belonging particularly to *Meliceritites* and *Elea*. Zooid-level characteristics, including eleozooid morphology, can be more similar between given species of *Reptomultelea* and erect species of these genera than with other species of *Reptomultelea*. For example, the intramural eleozooids of *R. pseudopalpebrosa* sp. nov. greatly resemble those of *Meliceritites palpebrosa* Levinsen, while the pointed eleozooids of *R. tuberculata* recall similar structures in *M.*

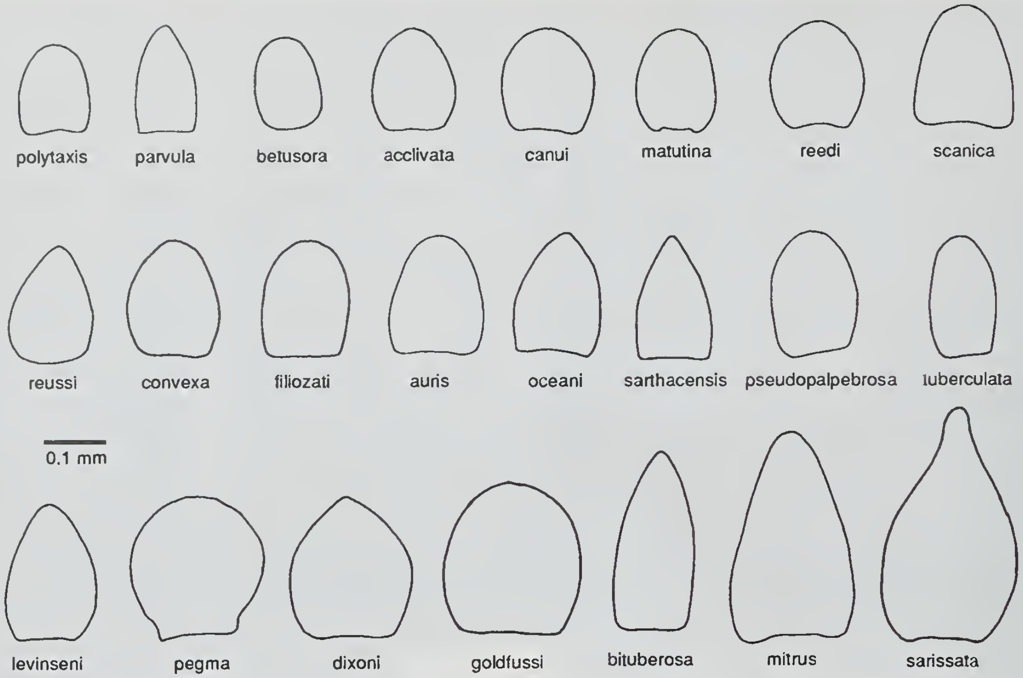


Fig. 125 Outlines of autozooidal aperture shapes in species of *Reptomultelea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

Fig. 126 Outlines of eleozooidal aperture shapes in species of *Reptomultelea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

gothica Levinsen and several related species of *Meliceritites*. Such similarities raise the possibility that *Reptomultelea* is not monophyletic but may instead be polyphyletic or paraphyletic. The polyphyletic hypothesis necessitates convergent evolution of species of *Reptomultelea* from various erect melicerititid species by parallel loss of the erect branches of colonies, together with enlargement of the encrusting colony base, seemingly a relatively simple evolutionary option. The paraphyletic hypothesis necessitates convergent evolution of species of erect melicerititids from the primitive 'genus' *Reptomultelea*. This is a less attractive alternative because (1) it demands the acquisition of erect growth several times, and (2) stratigraphical evidence suggests that *Reptomultelea* is not the most primitive melicerititid genus because the early Albian appearance of *Reptomultelea* post-dates the late Barremian appearance of *Meliceritites* by a significant time period. However, a full phylogenetic analysis of the melicerititids is needed to decide whether *Reptomultelea* is monophyletic, polyphyletic or paraphyletic. Until this has been accomplished, monophyly is assumed if only for reasons of nomenclatoral stability and pragmatic taxonomy.

Other genera established for encrusting melicerititids

Table 4 Key to the species of *Reptomultelea*. Note, because this key places a high reliance on eleozooids, which may not be developed in every specimen, identifications should be carefully checked against the full descriptions. Furthermore, it is possible that new material will reveal the presence of eleozooids in species in which they are currently unknown.

1.	Eleozooids present	2
	Eleozooids absent	20
2.	Eleozooid apertures larger than autozooids (i.e. rostrozooids)	3
	Eleozooid apertures smaller than autozooids	14
3.	Autozooid apertures very wide, more than 0·20 mm	4
	Autozooid apertures narrower, less than 0·20 mm	5
4.	Autozooid apertures ogee arch-shaped, more than 0·35 mm long	*R. sarissata* (p.94)
	Autozooid apertures very slightly pointed, less than 0·30 mm long	*R. dixoni* (p.69)
5.	Eleozooid rostrum broad, well-rounded distally	6
	Eleozooid rostrum narrow, pointed or poorly-rounded distally	10
6.	Opercula deeply depressed distally; apertural shelf very wide; eleozooid rostrum spatulate	*R. pegma* (p.85)
	Otherwise	7
7.	Zooids with a pair of prominent tubercles at either end of the hinge line	*R. bituberosa* (p.63)
	Otherwise	8
8.	Autozooid frontal wall short (less than 0·50 mm); aperture occupying a high proportion of the frontal area	*R. scanica* (p.95)
	Otherwise	9
9.	Eleozooid frontal wall longer than 0·85 mm	*R. oceani* (p.80)
	Eleozooid frontal wall shorter than 0·85 mm	*R. filiozati* (p.71)
10.	Autozooid apertures very tall (length about 1·5 × width); eleozooid apertures only slightly longer than autozooid apertures; kenozooids numerous	*R. tuberculata* (p.97)
	Otherwise	11
11.	Eleozooid rostrum well-raised distally so that plane of aperture is oblique to colony surface	*R. acclivata* (p.54)
	Otherwise	12
12.	Zooids very small – e.g. autozooid frontal wall width less than 0·21 mm; eleozooid frontal wall length less than 0·50 mm	*R. parvula* (p.82)
	Otherwise	13
13.	Zooids medium-sized – e.g. autozooid frontal wall length less than 0·59 mm; eleozooid frontal wall length less than 0·90 mm	*R. sarthacensis* (p.49)
	Zooids larger	*R. levinseni* (p.74)
14.	Eleozooid apertures inverted T-shaped (trifoliozooids)	15
	Otherwise	18
15.	Autozooids commonly with small kenozooids forming 'ears' on either side of the aperture	*R. auris* (p.57)
	Otherwise	16
16.	Autozooid frontal wall less than 0·45 mm long	*R. polytaxis* (p.85)
	Otherwise	17
17.	Autozooid aperture less than 0·15 mm wide	*R. betusora* (p.59)
	Autozooid aperture more than 0·15 mm wide	*R. convexa* (p.66)
18.	Eleozooid apertures D-shaped with a hood-like area distally	*R. pseudopalpebrosa* (p.89)
	Eleozooid apertures tall and pointed	19
19.	Autozooid apertures less than 0·20 mm wide	*R. canui* (p.65)
	Autozooid apertures more than 0·20 mm wide	*R. reussi* (p.91)
20.	Autozooid apertures less than 0·15 mm wide	*R. matutina* (p.77)
	Otherwise	21
21.	Autozooid apertures lancet arch-shaped	*R. mitrus* (p.79)
	Autozooid apertures rounded	22
22.	Autozooid apertures less than 0·21 mm long; crescentic arrangement of opercular pseudopores	*R. reedi* (p.91)
	Autozooid apertures more than 0·21 mm long; pseudopores scattered widely over operculum	*R. goldfussi* (p.73)

include *Reptelea* d'Orbigny, 1853, *Semimultelea* d'Orbigny, 1853, *Clausimultelea* d'Orbigny, 1853 and *Reptoceritites* Gregory, 1899. Lang (1906), who revised the 'reptant eleids', used *Reptelea* for unilamellar species lacking eleozooids ('avicularia'), *Reptoceritites* for unilamellar species with eleozooids, *Semimultelea* for bilamellar/multilamellar species lacking eleozooids, and *Reptomultelea* for bilamellar/multilamellar species with eleozooids (*Clausimultelea* he regarded as belonging to the non-melicerititid family Clausidae). The type species of *Reptelea*, *Reptelea pulchella* d'Orbigny, 1853, is of uncertain identity but may be the base of a colony of *Elea lamellosa* (d'Orbigny, 1850) (see p. 19), that of *Semimultelea*, *S. irregularis* d'Orbigny, 1853 is also the base of an *Elea lamellosa* colony (see p. 19), while that of *Reptoceritites*, *R. rowei* Gregory, 1899, is the base of a colony of *Meliceritites dollfusi* Pergens, 1890. Therefore, *Reptelea*, *Semimultelea* and *Reptoceritites* have no value as genera for the reception of non-erect melicerititid species as they all represent basal parts of erect taxa. Lang's (1906) scheme for the generic division of melicerititids must be rejected. *Clausimultelea*, type species *C. tuberculata* d'Orbigny (see p. 99), is merely a *Reptomultelea* with an above average proportion of kenozooids.

Semielea d'Orbigny, 1853, type species *S. vieilbanci* d'Orbigny, 1853 (see p. 43), is retained as a genus distinct from *Reptomultelea* despite the fact that cavariiform colonies of various species of *Reptomultelea* (e.g. *R. auris*, *R. convexa*, *R. reussi*) may closely resemble *Semielea*. These species of *Reptomultelea* show variable orientations of zooids in the initial layer whereas the zooids are orientated strictly parallel to the branch axis in *Semielea*. Furthermore, it is probable that cavariiform colonies of *Reptomultelea* grew loosely around erect organisms like hydroids (cf. many modern cavariiform cheilostomes). In contrast, the existence of 'platforms' partitioning the axial tubes shows that this was not the case in colonies of *Semielea*.

DISTRIBUTION. Lower Albian – Lower Campanian (Fig. 127), Europe and western Asia.

Reptomultelea sarthacensis d'Orbigny, 1853 Figs 2, 128–147

1826 *Cellepora escharoides* Goldfuss: 28 (partim), pl. 12, figs 3b–c only.
1853 *Reptelea sarthacensis* d'Orbigny: 640, pl. 604, figs 9–10, pl. 738, fig. 15.
1853 *Reptomultelea tuberosa* d'Orbigny: 655, pl. 741, figs 14–15.
1872 *Diastopora oceani* d'Orbigny; Reuss: 110 (partim), pl. 27, fig. 2 only.
1877 *Diastopora acupunctata* Novák: 99 (partim), pl. 6, fig. 1 only.
1890 *Semielea sarthacensis* (d'Orbigny); Pergens: 393.
1897*a* *Semielea sarthacensis* (d'Orbigny); Canu: 155, pl. 5, fig. 10.
1897*b* *Semielea sarthacensis* (d'Orbigny); Canu: 749.
non 1899 *Reptomultelea tuberosa* d'Orbigny; Gregory: 320, fig. 37 [=*Reptomultelea bituberosa* sp. nov., see p. 63].
1912 *Meliceritites sarthacensis* (d'Orbigny); Levinsen: 41, pl. 1, figs 1–2.
?1938 *Reptoceritites zahálkai* Prantl: 31, pl. 2, fig. 9.

MATERIAL. Holotype: MNHN d'Orbigny Collection 6562

(Fig. 129), Cenomanian, Le Mans, Sarthe, France; this colony encrusts a concavity in a sponge.

Other material: MNHN d'Orbigny Colln 6589 (Fig. 128), Cenomanian, Le Mans; presumed to be the holotype of *R. tuberosa*. PSUB Goldfuss Colln 105B, Cenomanian, Essen, Germany; presumed to be the specimen figured by Goldfuss (1826: pl. 12, figs 3b, c) as *Cellepora escharoides*. SMD un-numbered, specimen figured by Reuss (1872: pl. 27, fig. 2) as *Diastopora oceani* d'Orbigny (Voigt photocard 2814), Cenomanian, *plenus* Zone, Dresden-Plauen, Germany. EM RE 551.763.31.A711, Cenomanian, Essen. VH 10432, 10472, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany. VH 10437–8, top of Lower Cenomanian (*orbignyi* Zone) or base of Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, Calvados, France, Breton Colln. VH 10463, Lower Turonian, St Calais, Sarthe, France. VH 10466, Upper Cenomanian, St Calais. VH 10510, Upper Cenomanian (*plenus* Zone), Dresden-Plauen, Germany. BMNH D3624 (2 specimens), D3631, Cenomanian, Essener Grünsand, Essen, Westfalia, Germany. BMNH D4424 [only the specimen on a serpulid tube], Cenomanian [*plenus* Zone], Korycaner Schichten, Kamajk, Bohemia, Czechoslovakia. BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France, Voigt Colln. BMNH D54304–5, Upper Cenomanian (*plenus* Zone), Predboj, Bohemia, Czechoslovakia, Voigt Colln. BMNH D58952–8, Upper Cenomanian (*gourdoni* Zone), Craie glauconieuse à *Metiococeras* et *Sciponoceras*, St Calais road-cutting, Sarthe, Taylor & Hammond Colln.

Questionably assigned: BMNH D59244–6, Chloritic Marl, [Lower Cenomanian], St Catherine's Point, Isle of Wight, England.

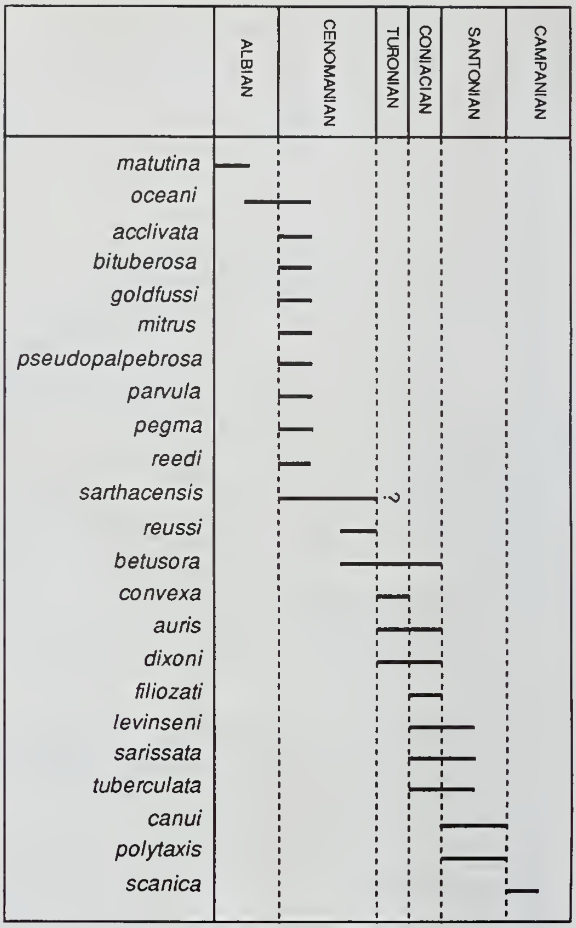


Fig. 127 Stratigraphical ranges of species of *Reptomultelea*.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 2), individual layers about 0·21–0·27 mm thick and occasionally growing free of the substratum with a transversely folded basal lamina. Ancestrula not identified unequivocally; autozooids from primary zone of astogenetic change with smaller, more rounded apertures than those from zones of repetition. Overgrowths (Figs 131, 141) originate by intrazooecial fission of one or more basal zooids; pseudoancestrula an autozooid, often surrounded by 6 daughter zooids, sometimes depressed beneath general level of colony surface but occasionally raised (possibly as a result of intramural budding); autozooids in secondary zone of astogenetic change with smaller and more rounded apertures than those in zone of repetition.

128

129

Figs 128, 129 *Reptomultelea sarthacensis* (d'Orbigny, 1853), photographs. 128, MNHN d'Orbigny Collection 6589, Cenomanian, Le Mans, France; presumed to be the holotype of *R. tuberosa* d'Orbigny, 1853; × 3·6. 129, MNHN d'Orbigny Collection 6562, Cenomanian, Le Mans, France; holotype of *Reptelea sarthacensis* d'Orbigny, 1853, showing autozooids, eleozooids and a gonozooid, × 18.

Organization fixed-walled. Zooids variably arranged, often approximately quincuncial.

Autozooids (Fig. 130) moderately small, frontally elongate, about 1·6–2 × longer than wide, often hexagonal in outline, occasionally diamond-shaped, with a pointed distal end; frontal wall occupying about half of the frontal surface, slightly convex, with circular pseudopores; boundary wall well-defined, salient. Aperture (Figs 132, 139) of medium size, on average about 1·5 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width somewhere between the hinge line and mid-length; apertural rim well-developed, raised to form a tubercle-like protuberance at the pointed distal end of the aperture; apertural shelf narrow; hinge line with low teeth at either end of a median bar. Operculum (Figs 133, 140) often preserved in-situ, convex, with about 24 radially ovoidal pseudopores arranged in a crescent close to the disto-lateral edge. Terminal diaphragms rarely present, located beneath level of apertural shelf, some with scattered pseudopores and a central depression. Intramural buds not observed.

Eleozooids (Figs 142–145) abundant, scattered; moderately large, frontal surface generally about 2·5 × longer than wide, considerably longer and usually a little wider than the autozooids; frontal wall occupying about half or less of the frontal surface, convex with pseudopores as in the autozooids. Aperture elongate, generally 2–3 × longer than wide, attaining maximum width at or a little distally of the hinge line, with a long, narrow rostral area sometimes a little spatulate; rostrum generally depressed at its distal end; hinge line with a wide median bar with small teeth at either end. Opercula rarely preserved in-situ. Terminal diaphragms (Fig. 142) may be present. Intramurally budded eleozooids (Fig. 145) and ?autozooids present.

Kenozooids variable in abundance, scattered or aggregated, often present immediately distal to eleozooids (Fig. 143) or in areas of disrupted growth (Figs 137, 146).

Gonozooids (Figs 146–147) moderately common, longitudinally elongate, 1·5–2 × longer than wide, a short parallel-sided portion emerging from the maternal aperture and becoming ovoidal to pear-shaped. Ooeciopore (Fig. 138) transversely elongate, variable in width, its distal edge indented internally by a hemiseptum. Atrial ring not observed.

MEASUREMENTS.
autozooids
(10 zooids from BMNH D54294)
frontal length: mean = 0·48 mm; SD = 0·026 mm; CV = 5·5; range = 0·44–0·51 mm
frontal width: mean = 0·26 mm; SD = 0·019 mm; CV = 7·2; range = 0·23–0·29 mm
apertural length: mean = 0·21 mm; SD = 0·017 mm; Q: CV = 8·0; range = 0·18–0·24 mm
apertural width: mean = 0·14 mm; SD = 0·012 mm; Q: CV = 8·6; range = 0·12–0·15 mm

(10 zooids from EM RE 551.763.31.A711)
frontal length: mean = 0·51 mm; SD = 0·035 mm; CV = 6·9; range = 0·48–0·59 mm
frontal width: mean = 0·25 mm; SD = 0·018 mm; CV = 7·1; range = 0·23–0·27 mm
apertural length: mean = 0·18 mm; SD = 0·022 mm; CV = 12·1; range = 0·15–0·23 mm
apertural width: mean = 0·13 mm; SD = 0·016 mm; CV = 12·8; range = 0·11–0·17 mm

(10 zooids from VH 10432)
frontal length: mean = 0·55 mm; SD = 0·030 mm; CV = 5·5; range = 0·51–0·59 mm
frontal width: mean = 0·27 mm; SD = 0·024 mm; CV = 8·8; range = 0·24–0·32 mm
apertural length: mean = 0·23 mm; SD = 0·017 mm; CV = 7·3; range = 0·21–0·26 mm
apertural width: mean = 0·15 mm; SD = 0·009 mm, CV = 5·7; range = 0·14–0·17 mm

eleozooids
(8 zooids from BMNH D54294)
frontal length: mean = 0·74 mm; SD = 0·054 mm; CV = 7·3; range = 0·68–0·83 mm
frontal width: mean = 0·29 mm; SD = 0·023 mm; CV = 7·7; range = 0·26–0·33 mm
apertural length: mean = 0·49 mm; SD = 0·041 mm; CV = 8·4; range = 0·44–0·54 mm
apertural width: mean = 0·19 mm; SD = 0·013 mm; CV = 6·5; range = 0·17–0·21 mm

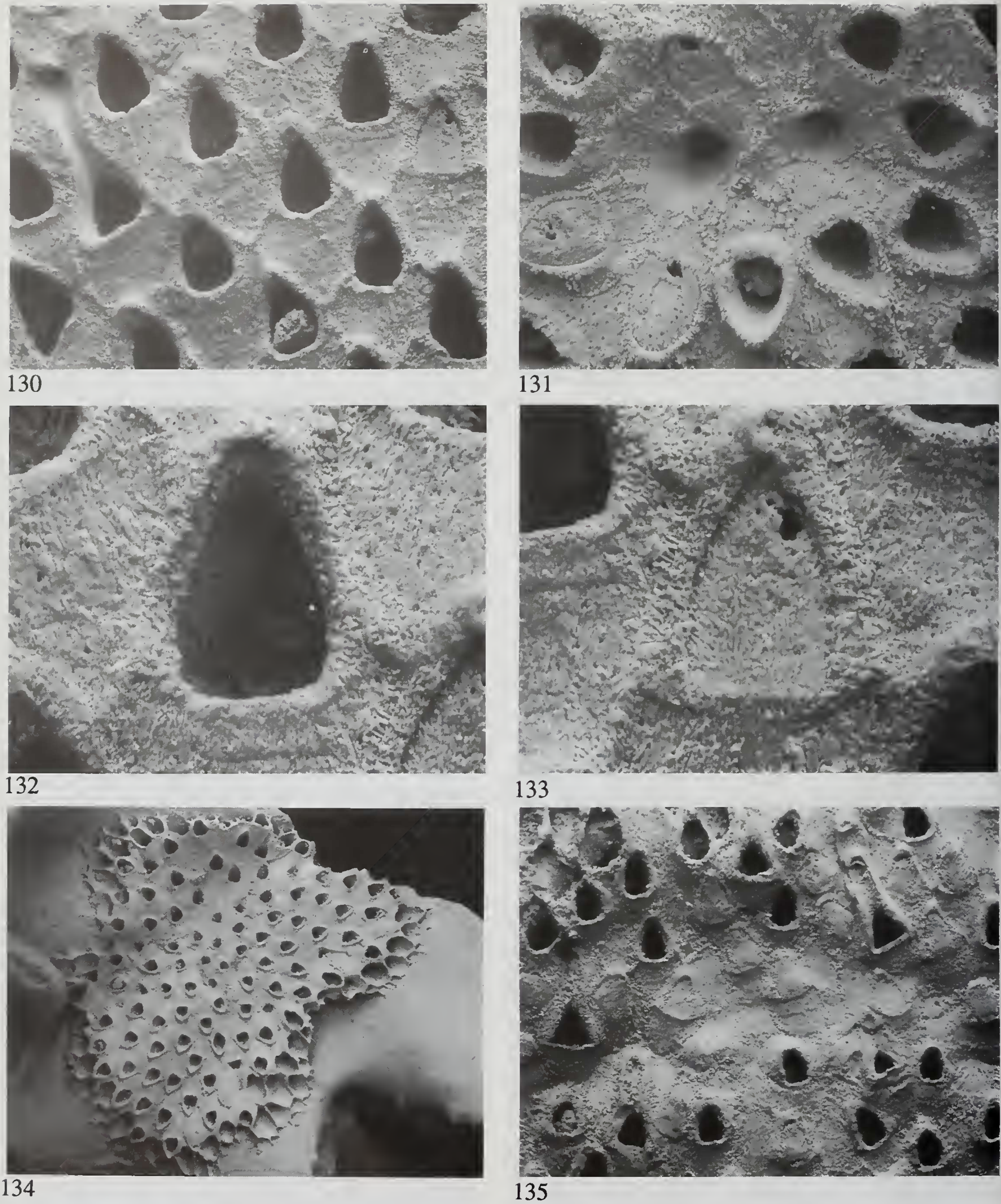
(7 zooids from EM RE 551.763.31.A711)
frontal length: mean = 0·81 mm; SD = 0·029 mm; CV = 3·6; range = 0·78–0·86 mm
frontal width: mean = 0·31 mm; SD = 0·036 mm; CV = 11·5; range = 0·27–0·38 mm
apertural length: mean = 0·50 mm; SD = 0·050 mm; CV = 10·1; range = 0·44–0·59 mm
apertural width: mean = 0·17 mm; SD = 0·029 mm; CV = 16·4; range = 0·15–0·23 mm

(8 zooids from VH 10432)
frontal length: mean = 0·70 mm; SD = 0·037 mm; CV = 5·3; range = 0·63–0·75 mm
frontal width: mean = 0·27 mm; SD = 0·017 mm; CV = 6·6; range = 0·24–0·30 mm
apertural length: mean = 0·38 mm; SD = 0·019 mm; CV = 5·1; range = 0·36–0·41 mm
apertural width: mean = 0·16 mm; SD = 0·011 mm; CV = 7·0; range = 0·15–0·18 mm

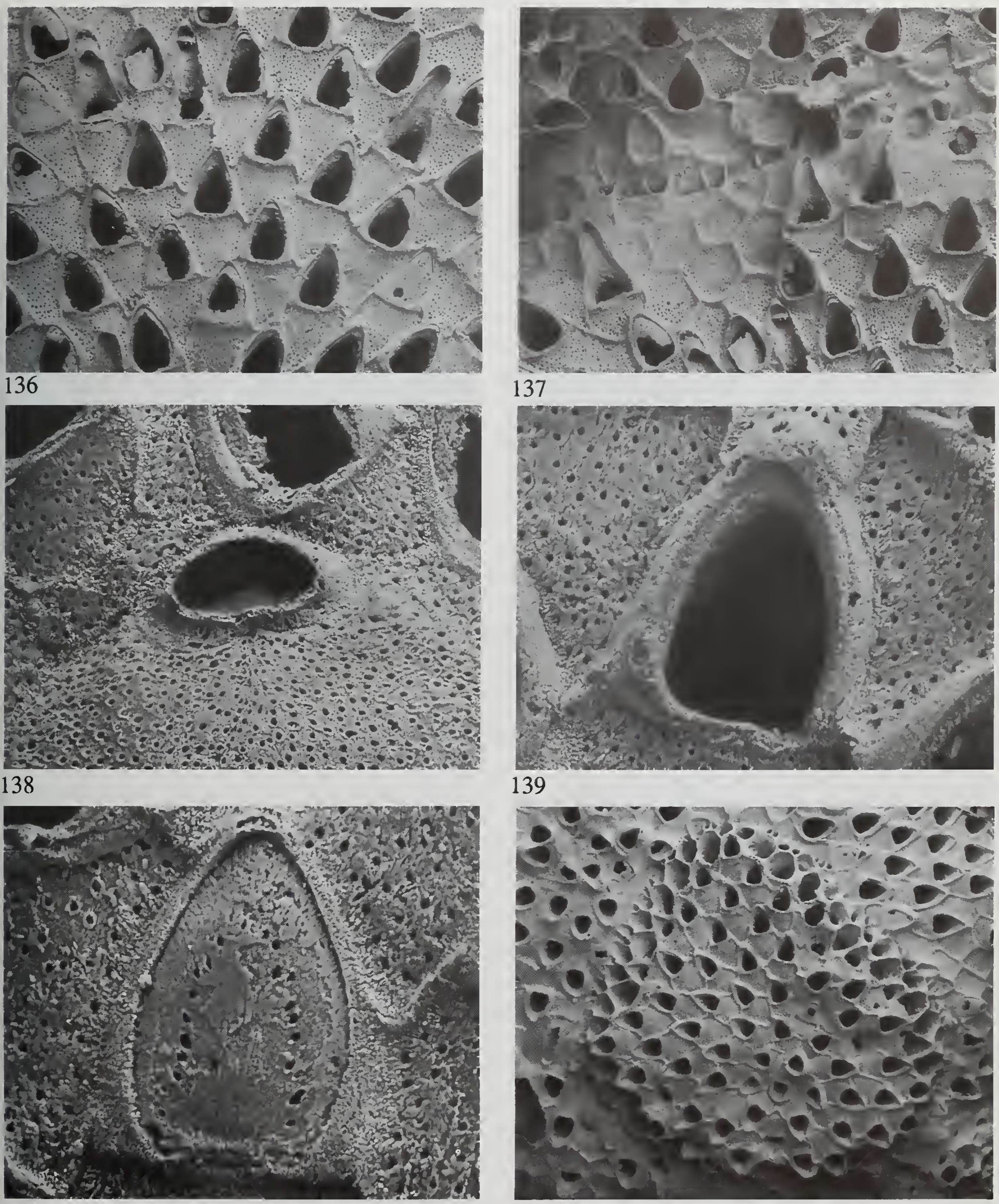
gonozooids
(1 zooid from holotype MNHN d'Orbigny Collection 6562)
frontal length: *ca* 1·43 mm
dilated frontal length: *ca* 1·30 mm
frontal width: *ca* 0·81 mm
ooeciopore length: *ca* 0·09 mm
ooeciopore width: *ca* 0·10 mm

(2 zooids from VH 10432)
frontal length: 1·58–1·74 mm
dilated frontal length: 1·37–1·53 mm
frontal width: 0·75–0·90 mm
ooeciopore length: 0·08 mm
ooeciopore width: 0·14–0·18 mm

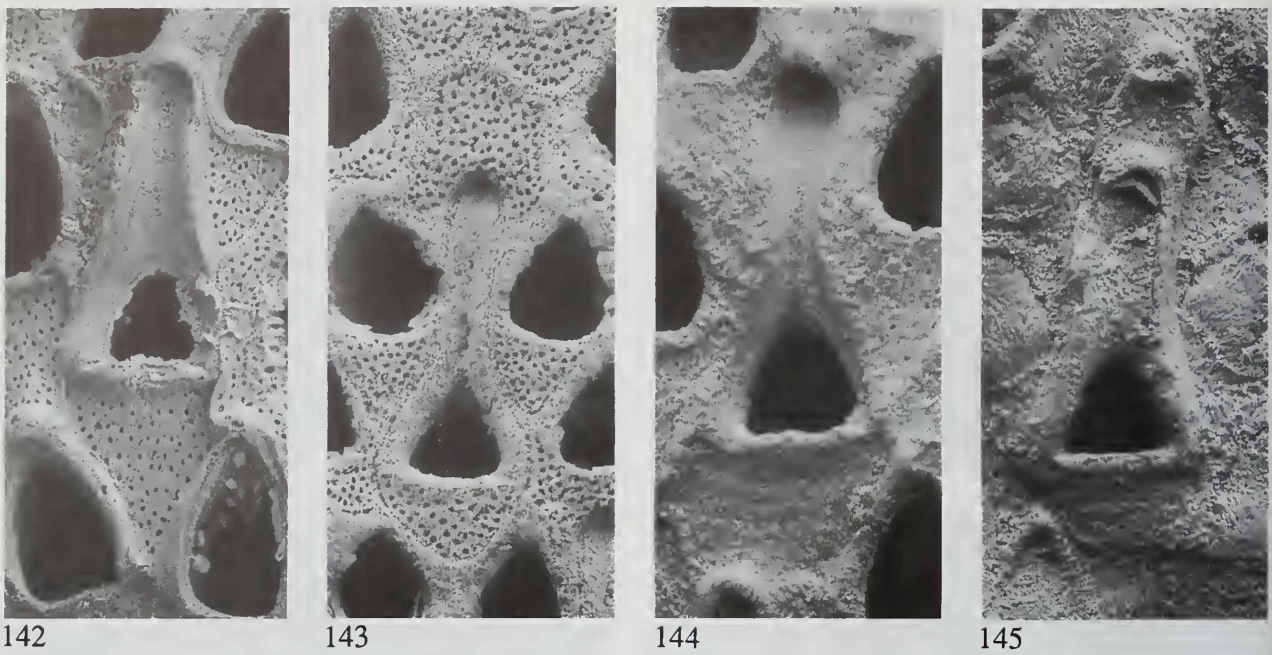
REMARKS. Pergens (1890) first recognized that *Reptomultelea tuberosa* d'Orbigny, 1853 was a junior synonym of *R. sarthacensis*, the latter species having been described in the same publication but with page priority. *R. tuberosa* is the type species, by monotypy, of *Reptomultelea* d'Orbigny, 1853, and therefore *R. sarthacensis* is considered to be the correct name for the type species of this genus. Gregory's (1899) *R. tuberosa* d'Orbigny is a different species, redescribed as *R. bituberosa* sp. nov. (p. 63).



Figs 130–135 *Reptomultelea sarthacensis* (d'Orbigny, 1853). 130–133, BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France; 130, autozooids and an eleozooid, × 72; 131, two depressed pseudoancestrulae surrounded by radiating autozooids, × 105; 132, autozooidal aperture, × 230; 133, autozooidal operculum, × 225. 134, VH 10463, Lower Turonian, St Calais, Sarthe, France; small colony encrusting a shell, × 15. 135, EM RE 551.763.31.A711, Cenomanian, Essen, Germany; depressed area of colony showing autozooids (with and without opercula) and eleozooids, × 35.



Figs 136–141 *Reptomultelea sarthacensis* (d'Orbigny, 1853), VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 136, autozooids (some with broken opercula) and eleozooids, × 48; 137, edge of overgrowth showing disrupted area with kenozooids and eleozooids, × 40; 138, ooeciopore, × 137; 139, autozooidal aperture, × 200; 140, autozooidal operculum, × 250; 141, newly-developed overgrowth, × 21.



Figs 142–145 *Reptomultelea sarthacensis* (d'Orbigny, 1853), variation in eleozooidal morphology. 142, VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; eleozooid with broad, almost parallel-sided rostrum and the remains of a terminal diaphragm, × 100. 143, VH 10510, Upper Cenomanian (*plenus* Zone), Dresden-Plauen, Germany; eleozooid with narrow, slightly spatulate rostrum resting on a distal kenozooid, × 75. 144, BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France; eleozooid with narrow, slightly spatulate rostrum, × 120. 145, EM RE 551.763.31.A711, Cenomanian, Essen, Germany; eleozooid with broad, slightly spatulate rostrum and hosting an intramural eleozooid, × 92.

The type specimen of *Reptoceritites zahálkai* Prantl, 1938, from the Turonian of Bohemia, was not available for study during a visit in June 1986 to the Narodni Museum, Prague, and Prantl's illustration of a worn specimen is inadequate for positive identification of the species. However, topotype specimens (BMNH D54304–5) collected by Professor E. Voigt are conspecific with *R. sarthacensis*.

One of the two specimens (SMD un-numbered; Voigt photocard 2814) from the *plenus* Zone of Dresden figured by Reuss (1872) as *Diastopora oceani* d'Orbigny appears to be a unilamellar colony of *R. sarthacensis* encrusting an oyster (pl. 27, fig. 2). Pergens (1890: p. 399) recognized that the *D. oceani* of Reuss was not the same as d'Orbigny's species and proposed *Semielea reussi* for *D. oceani* sensu Reuss. *S. reussi* is not placed in synonymy with *R. sarthacensis* because the second of Reuss's syntype specimens (pl. 27, fig. 3) is a different species and is here selected as the lectotype of *S. reussi* (see p. 91).

Among the material described from the Czechoslovakian Cenomanian/Turonian as *Diastopora acupunctata* Novák, 1877, is at least one specimen belonging to *R. sarthacensis*. This is the specimen shown in plate 6, fig. 1 of Novák (1877) and registered in the Narodni Museum as 2437 (Voigt photocards 6455 and 6458).

As here delimited, *R. sarthacensis* is a widely distributed species ranging from the Lower Cenomanian to the Upper Cenomanian or possibly Lower Turonian. Some morphometric differences exist between populations, but the unity of the species is supported by the ubiquitous long, narrow eleozooid rostra and gothic arch-shaped autozooid apertures with distally raised rims. Colonies from the Lower Cenomanian of Westfalia tend to have eleozooid rostra rather broader than those of younger populations, and an above average proportion of kenozooids occurs in specimens from the Essener Grünsand. The short but variable length of the eleozooid rostra in material from the Lower Cenomanian of the Isle of Wight (BMNH D59244–6) could be due to environmental stunting or might indicate a specific distinction; therefore, these specimens are questionably assigned to *R. sarthacensis*.

Reptomultelea levinseni sp. nov. (p. 74) from the Coniacian/Santonian of northern France is very similar to *R. sarthacensis* but has appreciably longer autozooid and eleozooid frontal walls.

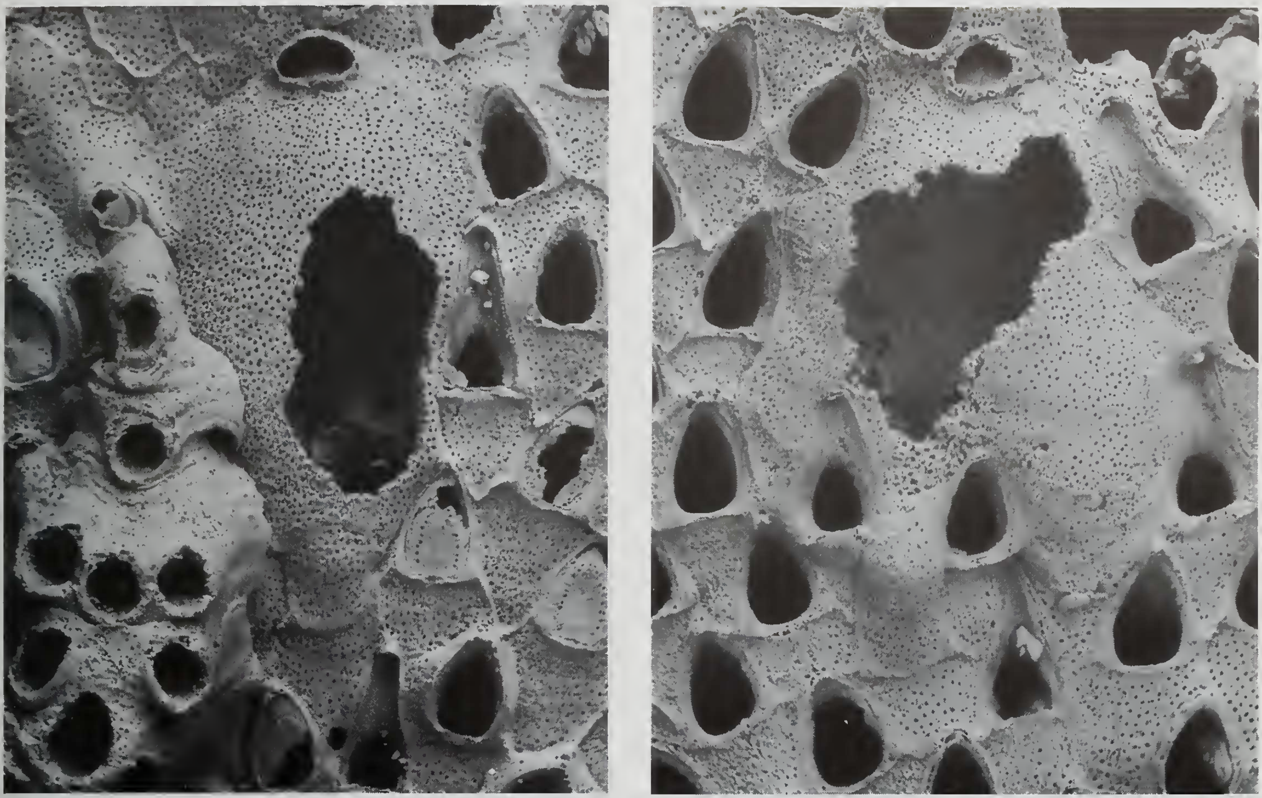
DISTRIBUTION. Lower Cenomanian-Upper Cenomanian or Lower Turonian. Known from the Lower Cenomanian of Germany, ?France and ?England; ?Middle Cenomanian of France; Upper Cenomanian of Germany, France and Czechoslovakia.

Reptomultelea acclivata sp. nov. Figs 148–154

MATERIAL. Holotype: VH 10427, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany. Paratype: VH 10502, same horizon and locality as holotype. Other material: VH un-numbered, several topotype colonies.

NAME. Acclivata, Latin for upward slope, with reference to the upward-sloping eleozooid rostra.

DESCRIPTION. Colony unilamellar or multilamellar, each



146 147

Figs 146, 147 *Reptomultelea sarthacensis* (d'Orbigny, 1853), gonozooids, VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 146, gonozooid with broken frontal wall; note fouling tubuliporine cyclostome which has become enveloped proximally by an overgrowth of melicerititid kenozooids, × 60; 147, two coalescent gonozooids sharing a single ooeciopore, × 70.

layer about 0·23 mm thick, often growing free of the substratum and with a transversely folded basal lamina. Ancestrula not observed. Overgrowths (Figs 148–149) presumed to originate by intrazooecial fission; pseudoancestrulae with depressed apertures, small (*ca* 0·08–0·09 mm), more or less equidimensional and less pointed than apertures of autozooids from zone of astogenetic repetition. Organization fixed-walled. Zooids arranged in irregular quincunx.

Autozooids (Figs 150, 152) small, frontally elongate, about twice as long as wide, subhexagonal with a moderately pointed distal end; frontal wall generally occupying more than half of frontal surface, pseudopores subcircular; boundary wall poorly defined, subdued. Aperture of small size, slightly elongate, about 1·1–1·2 × longer than wide, widest between the hinge line and mid-length, slightly arched to rounded distally; apertural rim well-developed distally where it may be prolonged into a pointed projection; hinge line bowed, detailed structure unclear; apertural shelf very narrow or absent. Operculum (Fig. 151) sometimes preserved in-situ, flat centrally but with slightly convex sides, possessing about 20 slit-like pseudopores arranged in a crescent parallel to the disto-lateral edge; inner surface with narrow sclerites forming a low arch across the distal edge of the operculum where they are joined. Terminal diaphragms and intramural buds not observed.

Eleozooids (Figs 148, 150, 152–153) numerous, scattered; small, frontally elongate, about twice as long as wide, a little longer and wider than the autozooids; frontal wall occupying about half of the frontal surface, pseudopores circular and present in about the same density as in the autozooids. Aperture elongate, about twice as long as wide, attaining maximum width close to the hinge line. Rostrum (Fig. 153) long and narrow; in some eleozooids flat, but in most well raised distally, standing above the colony surface by as much as 0·3 mm, so that plane of aperture is inclined by up to 60° to the colony surface, and often with a terminal hook directed proximally. Opercula observed in situ only in overgrown zooids; inner surface of displaced opercula seemingly with marginal sclerites. Apparent intramurally budded eleozooids have thickened rostra and shortened apertures.

Kenozooids occasionally present.

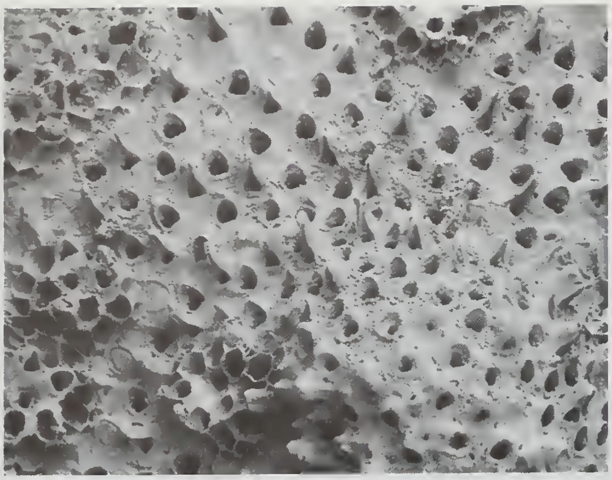
Gonozooids (Fig. 154) present in paratype (VH 10502), frontally almost twice as long as wide, the bulbous distal part being ovoidal or pear-shaped. Ooeciopore (Fig. 153) variably transversely elongate, the ooeciostome sometimes reflexed proximally. Atrial ring not observed.

Measurements.

autozooids (10 zooids from holotype VH 10427)

frontal length: mean = 0·44 mm; SD = 0·038 mm; CV = 8·7; range = 0·38–0·53 mm

frontal width: mean = 0·22 mm; SD = 0·012 mm;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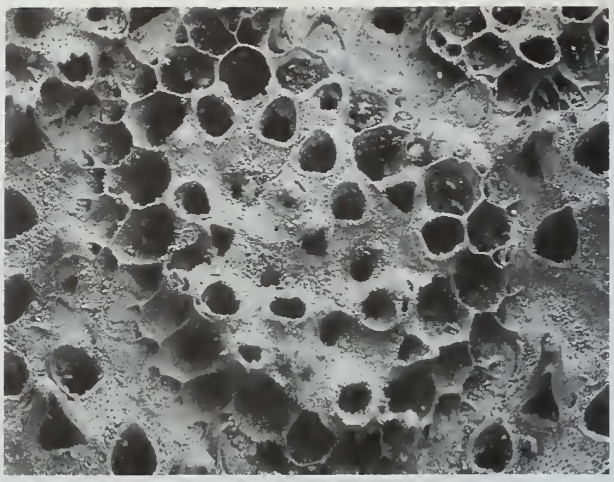
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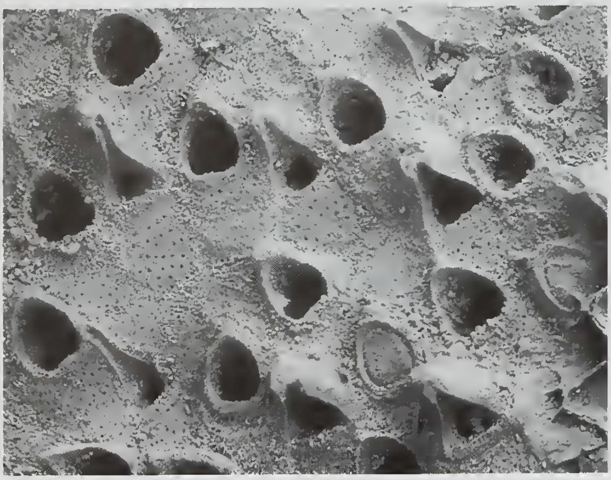
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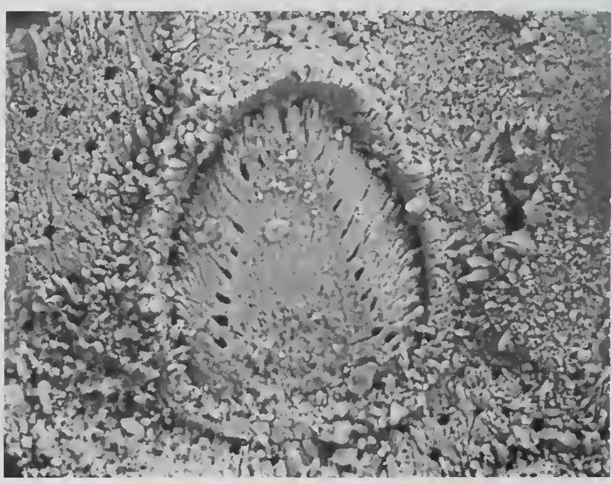
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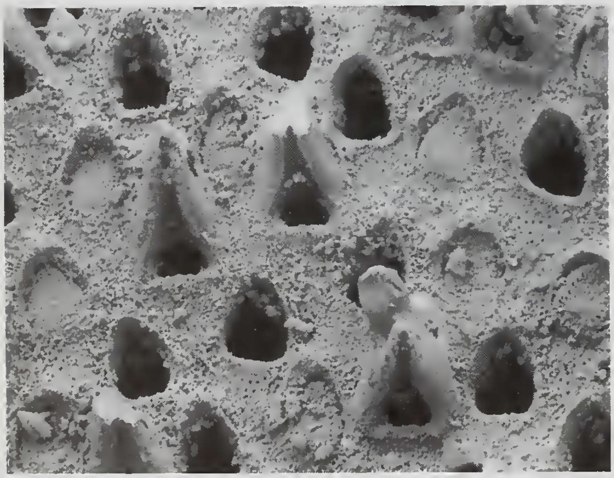
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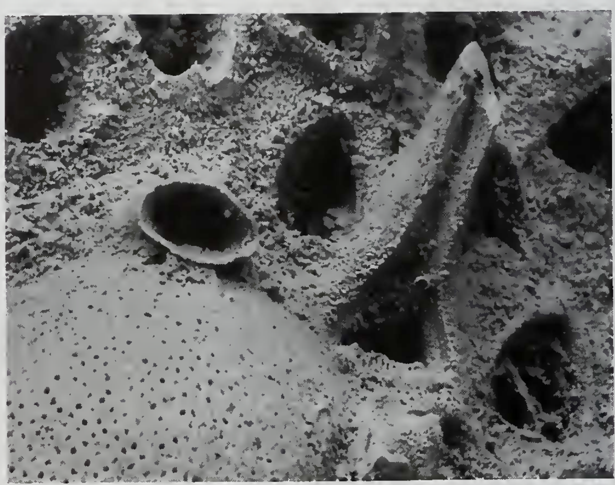
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Figs 148–153 *Reptomultelea acclivata* sp. nov. 148–151, VH 10427, holotype, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 148, colony surface showing prominent eleozooids and overgrowths, × 22; 149, small overgrowth, × 40; 150, autozooids and eleozooids, × 55; 151, autozooidal operculum, × 250. 152–153, VH 10502, Lower Cenomanian, Mülheim-Broich; 152, autozooids and eleozooids with distally-raised rostra, × 62; 153, ooeciopore and an eleozooid with long, raised rostrum, × 115.

CV = 5·6; range = 0·21–0·24 mm
apertural length: mean = 0·17 mm; SD = 0·011 mm; CV = 6·7; range = 0·15–0·18 mm
apertural width: mean = 0·15 mm; SD = 0·007 mm; CV = 5·0; range = 0·14–0·15 mm

eleozooids (9 zooids from holotype VH 10427)
frontal length: mean = 0·48 mm; SD = 0·029 mm; CV = 6·1; range = 0·44–0·53 mm
frontal width: mean = 0·24 mm; SD = 0·020 mm; CV = 8·2; range = 0·21–0·27 mm
apertural length: mean = 0·28 mm; SD = 0·055 mm; CV = 19·6; range = 0·21–0·38 mm
apertural width: mean = 0·14 mm; SD = 0·016 mm; CV = 11·5; range = 0·11–0·15 mm
[nb. apertural length measured in the plane of the aperture, i.e. obliquely to the colony surface]

gonozooid (6 zooids from holotype VH 10427)
frontal length: mean = 1·50 mm; SD = 0·056 mm; CV = 3·7; range = 1·44–1·59 mm
distal frontal wall length mean = 1·30 mm; SD = 0·044 mm; CV = 3·4; range = 1·25–1·35 mm
frontal width: mean = 0·84 mm; SD = 0·046 mm; CV = 5·5; range = 0·80–0·90 mm
ooeciopore length: mean = 0·08 mm; SD = 0·006 mm; CV = 7·9; range = 0·08–0·09 mm
ooeciopore width: mean = 0·14 mm; SD = 0·028 mm; CV = 21·1; range = 0·11–0·17 mm

REMARKS. This new species resembles *Reptomultelea sarthacensis* (d'Orbigny) and *R. parvula* sp. nov., with which it co-occurs at Mülheim. However, it differs in having abundant eleozooids with distally raised rostra, causing the plane of the aperture to be at a considerable angle to the colony surface and the colony to have a spiny appearance. In well-preserved specimens the distal ends of the rostra are slightly hooked, a feature unique to *R. acclivata* among melicerititids. Autozooid apertures are less elongate than in *R. sarthacensis* and larger than in *R. parvula*.

Fig. 154 *Reptomultelea acclivata* sp. nov., VH 10502, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany, gonozooid, × 70.

The holotype colony evidently encrusted a fragment of a dendroid cyclostome, grew free beyond its initial substratum (as with many other colonies of *Reptomultelea* spp. from Mülheim), and incorporated secondary substrates, including an onychocellid cheilostome bryozoan, into its base.

DISTRIBUTION. Lower Cenomanian of Mülheim, Westfalia, Germany.

Reptomultelea auris sp. nov. Figs 155–162

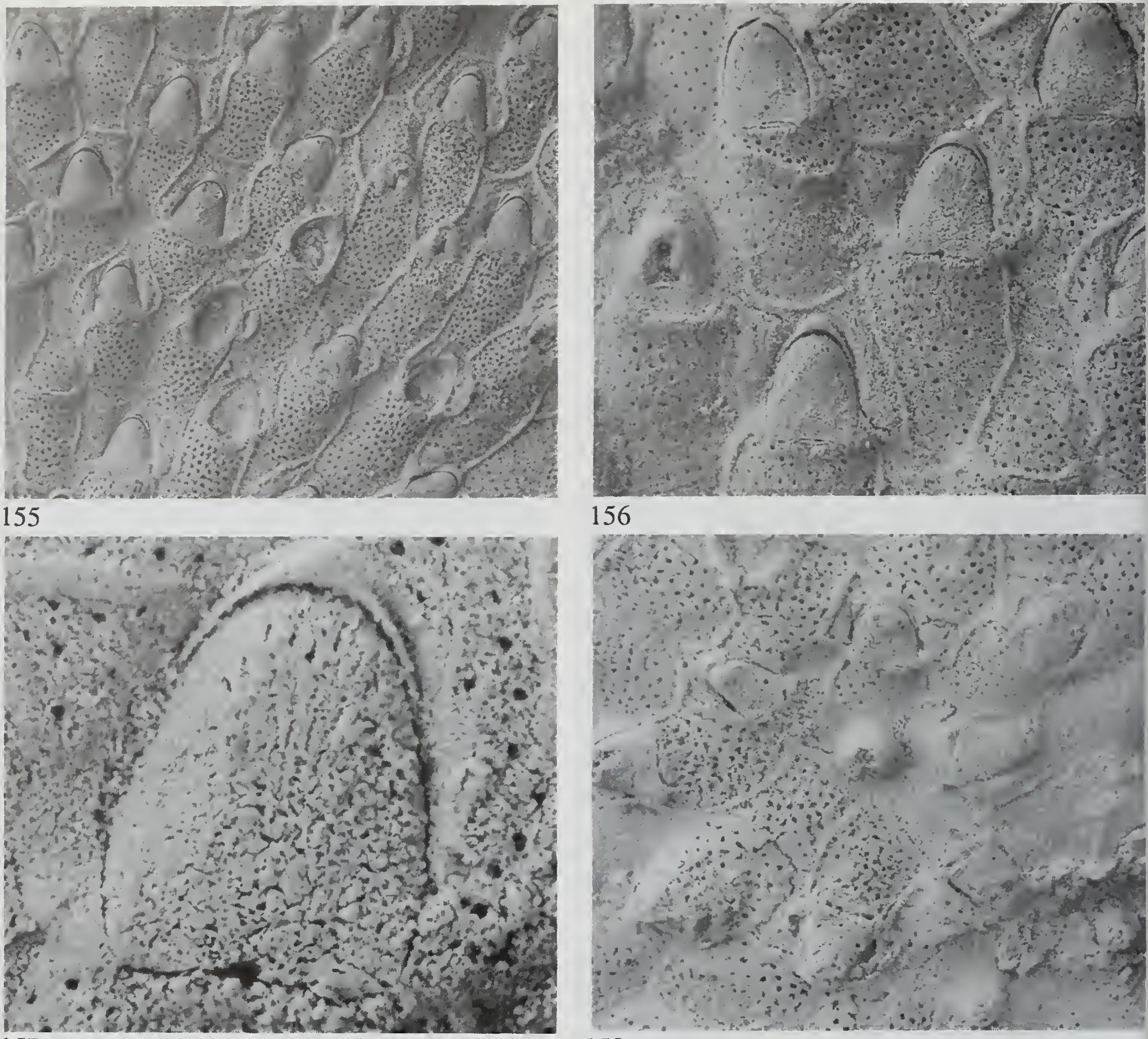
MATERIAL. Holotype: BMNH D46049, Turonian, *lata* Zone, Ballard Point, Dorset, England, A.W. Rowe Collection.

Paratypes: BMNH D46048, D46052, same details as holotype. D43694, [Coniacian], *M. cortestudinarium* Zone, Seaford Head, Sussex, England, A.W. Rowe Colln. D46027, Turonian, *planus* Zone, White Nothe, Dorset, England, A.W. Rowe Colln. BZ 1005–6, Turonian, *planus* Zone Chalk, Tilleul Beach, Seine Maritime, France, Taylor and Hammond Colln, 1985. BZ 1007, Coniacian, Craie á *M. normanniae*, above Tilleul No. 3 Hardground (see Kennedy and Juignet, 1974), Etretat, Seine Maritime.

NAME. Auris, Latin for ear, with reference to the paired kenozooids which resemble ears on either side of the autozooidal aperture.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·3 mm thick, generally (?always) cavariiform with tubular branches 5–10 mm in diameter, up to 40 mm in maximum observed length, flexuous and occasionally bifurcating; basal lamina on inside of tubes with transverse undulations, apparently growing freely of a substratum. Overgrowths (Fig. 158) originate by intrazooecial fission; pseudoancestrula an autozooid, aperture depressed, small, about 0·11–0·12 mm long by 0·08 mm wide, surrounded by approximately 6 periancestrular buds initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged roughly in quincunx away from overgrowth origins and anastomoses.

Autozooids (Figs 155–156, 159, 161) of large size, frontally elongate, usually a little over twice as long as wide, subhexagonal or subrhomboidal in outline, subacuminate distally; frontal wall convex, pseudopores circular; boundary wall salient. Aperture (Fig. 160) of moderate size, longitudinally elongate, on average 1·1–1·2 × longer than wide, attaining maximum width just distal to the hinge line, arched distally; apertural rim narrow; apertural shelf moderately wide distally, tapering proximally; hinge line bowed, raised slightly so that plane of aperture faces distally. Operculum (Figs 157, 162) often preserved in-situ, convex; pseudopores slightly radially elongate, numbering about 20, arranged close to and parallel with the distal edge of the operculum. Terminal



Figs 155–158 *Reptomultelea auris* sp. nov., BMNH D46049, holotype, Turonian, *lata* Zone, Ballard Point, Dorset, England; 155, autozooids, eleozooids and kenozooids, × 35; 156, operculate autozooids, kenozooids, intramural eleozooid (left), and evidence of regeneration after damage in upper left autozooid, × 72; 157, autozooidal operculum, × 240; 158, overgrowth origin, × 56.

diaphragms not observed. Intramurally budded eleozooids (Fig. 156) common, apertures trifoliate like those of primary eleozooids, elevated distally so that plane of aperture faces proximally.

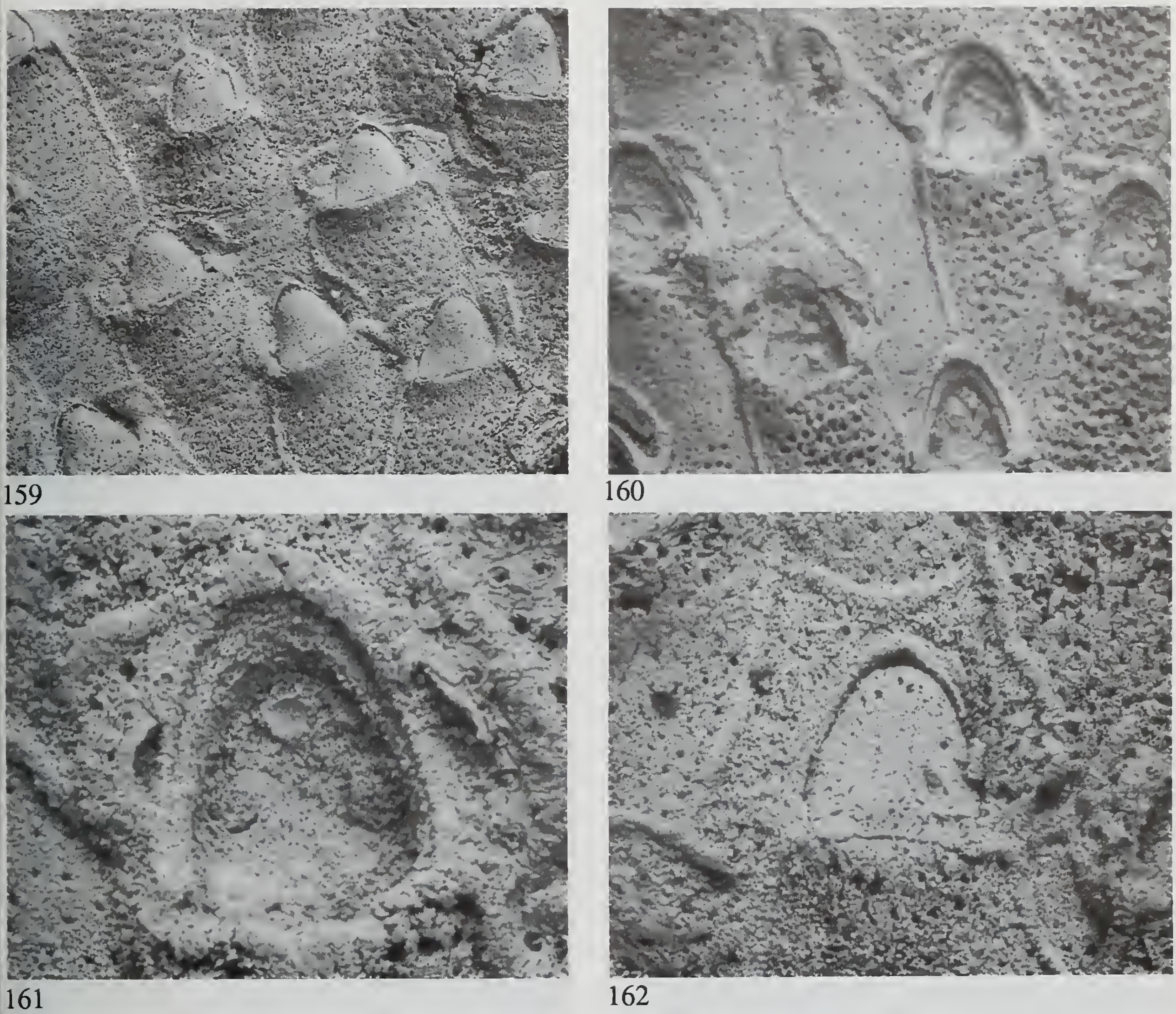
Kenozooids (Figs 155–156) abundant, small, commonly paired on either side of the autozooidal apertures and semicircular or crescent-shaped in outline.

Eleozooids (Fig. 161) infrequent, scattered, frontally elongate, typically slightly longer but narrower than the autozooids, narrow and pointed distally. Aperture small, longitudinally elongate, trifoliate in outline, about twice as long as wide, considerably shorter and narrower than autozooidal apertures; apertural rim moderately raised. Opercula not observed. Intramural buds unknown.

Gonozooids known from a single broken example which is missing the proximal part; frontal shape apparently subcircular. Ooeciopore transversely elliptical, slightly more than 2 × wider than long. Atrial ring present.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype BMNH D46049)

frontal length:	mean = 0·66 mm; SD = 0·069 mm; CV = 10·4; range = 0·54–0·78 mm
frontal width:	mean = 0·28 mm; SD = 0·025 mm; CV = 8·7; range = 0·26–0·33 mm
apertural length:	mean = 0·20 mm; SD = 0·008 mm; CV = 3·8; range = 0·20–0·21 mm
apertural width:	mean = 0·17 mm; SD = 0·011 mm; CV = 6·1; range = 0·15–0·18 mm



Figs 159–162 *Reptomultelea auris* sp. nov., 159, BZ 1005, Turonian, *planus* Zone Chalk, Tilleul Beach, Seine Maritime, France, operculate autozooids with small kenozooids lateral to the opercula, × 82. 160–162, BMNH D46049, holotype, Turonian, *lata* Zone, Ballard Point, Dorset, England; 160, autozooidal aperture, × 182; 161, autozooids and primary eleozooid, × 65; 162, autozooidal operculum bordered distally and laterally by a kenozooid, × 125.

eleozooids (3 zooids from holotype BMNH D46049)

frontal length:	range = 0·65–0·87 mm
frontal width:	range = 0·24–0·29 mm
apertural length:	range = 0·12–0·14 mm
apertural width:	range = 0·06–0·08 mm

gonozooid (1 incomplete zooid from BMNH BZ1006)

frontal width:	*ca* 1·13 mm
ooeciopore length:	0·09 mm
ooeciopore width:	0·20 mm

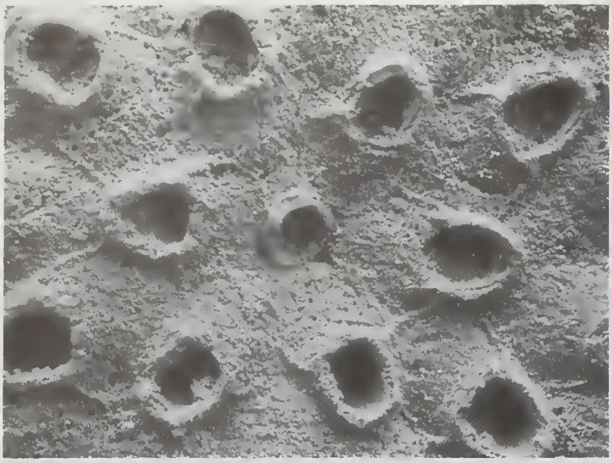
REMARKS. Zooidal dimensions in this new species are similar to *Reptomultelea canui* (Voigt), but *R. auris* differs in having autozooidal apertures more pointed distally and inclined slightly in a distal direction, and also in the presence of common small kenozooids on either side of the autozooidal apertures. These 'ear-like' paired kenozooids are not ubiquitous but are associated with a significant proportion of autozooids in all colonies of *R. auris*. They provide the most useful means of recognizing the species, being known only from this species among melicerititids.

The cavariiform morphology (*sensu* Brood, 1972) of *R. auris* colonies with free-growing basal laminae suggests loose growth of colonies around, but not directly encrusting, arborescent organisms. Modern colonies of *Schizoporella* and other cheilostomes show a similar morphology when growing loosely around clusters of hydroid stems or other erect substrates.

DISTRIBUTION. Upper Turonian-Coniacian of southern England and northern France.

Reptomultelea betusora nom. nov. Figs 163–173

?1846 *Diastopora confluens* Reuss: 65, pl. 15, figs 41, 42.
1874 *Diastopora tuberosa* Reuss: 132, pl. II. 25, figs 2 and 3.
1877 *Diastopora acupunctata* Novák: 99 (partim), pl. 6,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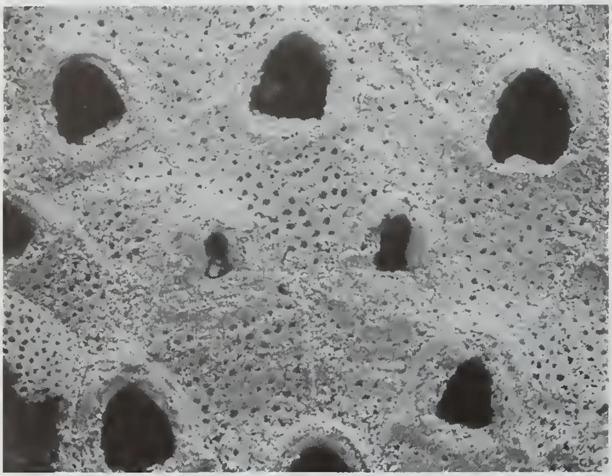
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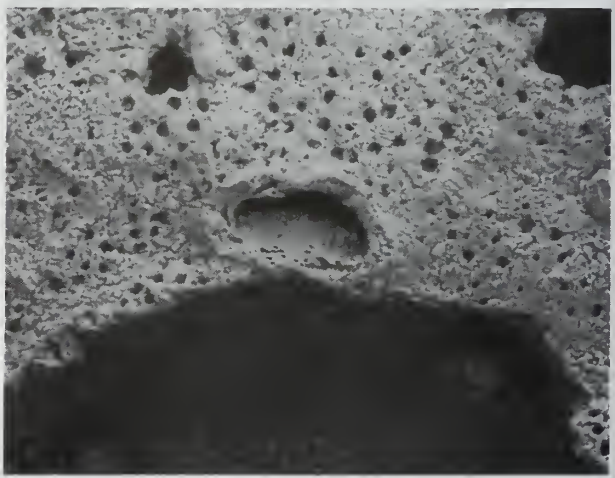
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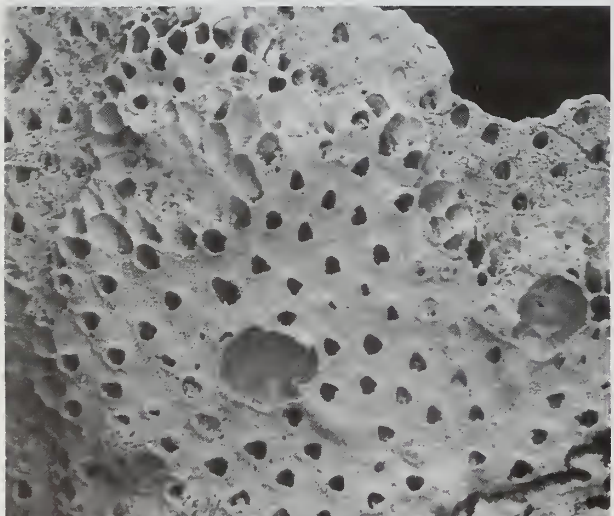
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168

Figs 163–168 *Reptomultelea betusora* nom. nov. 163–164, SMD un-numbered, lectotype, Turonian, Strehlen, Dresden, Germany; 163, pseudoancestrula surrounded by radiating autozooids, × 80; 164, oblique view showing four eleozooids, × 100. 165–167, VH 10436, Upper Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia; 165, autozooids and intramural eleozooids, × 100; 166, ooeciopore, × 180; 167, general view of colony with two broken gonozooids, × 21. 168, BMNH BZ 1000 Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground, Etretat, Seine-Maritime, France, part of large colony, × 22.

figs 2–5, ?figs 6–14 [non fig. 1 = *R. sarthacensis*].
?1877 *Diastopora acupunctata* Novak; Fric: 93, 146, fig. 149.
?1883 *Diastopora acupunctata* Novak; Fric: 81, 124, 125, fig. 104.
?1892 *Semielea acupunctata* (Novák); Pocta: 29, pl. 2, fig. 16.
1899 *Semimultelea acupunctata* (Novák); Gregory: 297.

MATERIAL. Lectotype: SMD un-numbered, the specimen figured here as Figs 163, 164, Turonian, Strehlen, Dresden, Germany. Paralectotypes: SMD un-numbered, 2 specimens n same sample as lectotype.

Other material: VH 10436, Upper Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia. BMNH BZ 999, Cenomanian [*plenus* Zone], Korycaner Schichten, Kamajk, Bohemia, Czechoslovakia, Fric Colln. D58949–50, Turonian, *nodosoides* Zone, Craie á *Inoceramus labiatus*, St Calais road-cutting, Sarthe, France, Taylor & Hammond Colln 1985. BZ 1000–4, Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground (see Kennedy & Juignet, 1974), Etretat, Seine-Maritime, France, Taylor & Hammond Colln 1985.

NAME. An anagram of *tuberosa*.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·35–0·40 mm thick, sometimes growing freely and with a transversely wrinkled basal lamina. Ancestrula not observed. Overgrowths originate by intrazooecial fission; pseudoancestrula (Fig. 163) usually an autozooid (aperture *ca* 0·10 × 0·08 mm diameter), sometimes an eleozooid, surrounded by about 6 daughter buds which initiate a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures variably arranged, often n irregular quincunx.

Autozooids (Figs 165, 169) medium-sized, frontally elongate, on average about twice as long as wide, often hexagonal or rhomboidal in outline, rounded distally. Frontal wall slightly convex, occupying about two-thirds of the frontal surface, slightly convex; boundary wall salient. Aperture (Fig. 172) small, elongate, about 1·2–1·5 × longer than wide, attaining maximum width about mid-length, moderately rounded distally; apertural rim raised slightly, especially distally; apertural shelf narrow, tapering proximally. Operculum (Fig. 170) seldom preserved n-situ, convex with a crescent of elongate pseudopores. Terminal diaphragms not observed. Intramurally budded eleozooids (Figs 165, 171) frequent, intramural autozooids not seen.

Kenozooids present in varying numbers, sometimes abundant and clustered.

Eleozooids (Figs 164, 169, 171) common; frontal surface generally a little smaller than autozooids but similar in overall proportions, although much narrower distally in the apertural region. Aperture elongate, on average about twice as long as wide, considerably smaller than an autozooidal aperture, inverted T-shaped in outline because of ndentation by rostral shelf, often set in a plane oblique to the colony surface and directed proximally. Operculum not observed in-situ.

Gonozooids (Figs 167, 173) known only from specimen VH 10436, which has two, both budded close to the origin of an overgrowth. Frontally relatively small, elongate, about twice as long as wide, the distal inflated frontal wall emerging from the maternal aperture, initially parallel-sided before dilating and becoming ovoidal. Ooeciopore (Fig. 166) transversely elongate, indented by a proximal hemiseptum. Atrial ring present. Floor of gonozooid has salient outlines of underlying zooids beneath proximal part of dilated frontal wall, smoother distally.

MEASUREMENTS.
autozooids
(10 zooids from VH 10436)

frontal length:	mean = 0·45 mm; SD = 0·042 mm; CV = 9·5; range = 0·39–0·53 mm
frontal width:	mean = 0·21 mm; SD = 0·019 mm; CV = 8·8; range = 0·20–0·24 mm
apertural length:	mean = 0·14 mm; SD = 0·009 mm; CV = 6·9; range = 0·12–0·15 mm
apertural width:	mean = 0·11 mm; SD = 0·008 mm; CV = 7·0; range = 0·11–0·12 mm

(10 zooids from BMNH BZ 1000)

frontal length:	mean = 0·54 mm; SD = 0·040 mm; CV = 7·4; range = 0·50–0·63 mm
frontal width:	mean = 0·28 mm; SD = 0·020 mm; CV = 7·0; range = 0·26–0·32 mm
apertural length:	mean = 0·16 mm; SD = 0·014 mm; CV = 9·1; range = 0·14–0·18 mm
apertural width:	mean = 0·12 mm; SD = 0·009 mm; CV = 7·0; range = 0·11–0·14 mm

eleozooids
(VH 10436)

frontal length:	*ca* 0·35–0·38 mm
frontal width:	*ca* 0·18–0·20 mm
apertural length:	*ca* 0·06–0·08 mm
apertural width:	*ca* 0·05 mm

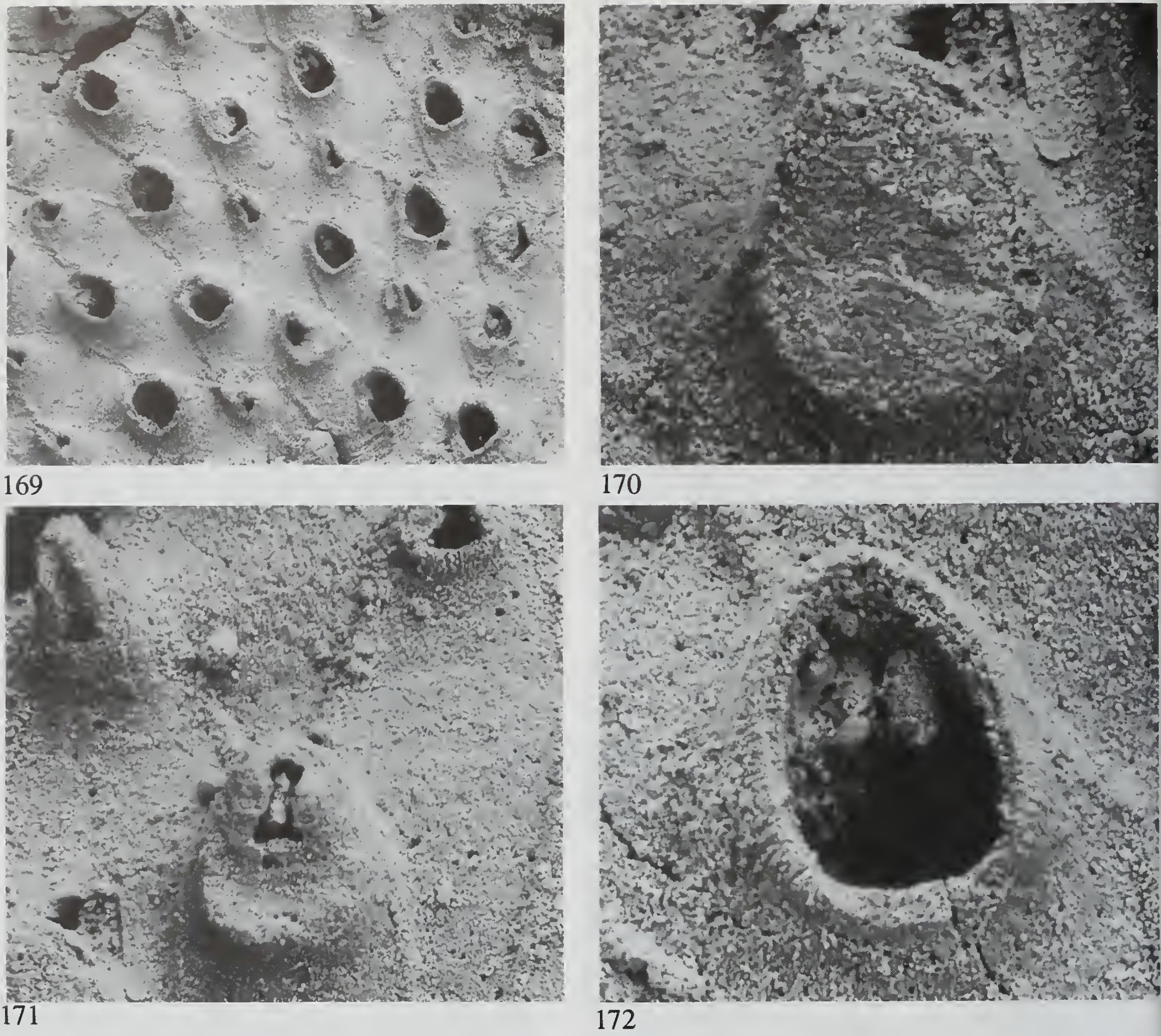
(5 zooids from BMNH D59329)

frontal length:	mean = 0·50 mm; SD = 0·048 mm; CV = 9·6; range = 0·42–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·017 mm; CV = 6·6; range = 0·24–0·29 mm
apertural length:	mean = 0·09 mm; SD = 0·024 mm; CV = 26·4; range = 0·06–0·12 mm
apertural width:	mean = 0·04 mm; SD = 0·008 mm; CV = 21·1; range = 0·03–0·05 mm

gonozooids (2 zooids from VH 10436)

frontal length:	1·20–1·29 mm
distal frontal wall length:	0·99–1·11 mm
frontal width:	0·53–0·68 mm
ooeciopore length:	0·06 mm
ooeciopore width:	0·09–0·11 mm

REMARKS. Reassignment of the Reuss (1874) species *tuberosa* from *Diastopora* to *Reptomultelea* makes it a secondary junior homonym of *Reptomultelea tuberosa* d'Orbigny, 1853. Although the latter species, which is the type species of *Reptomultelea*, is a subjective junior synomym of *R. sarthacensis* d'Orbigny, 1853 (see p. 51), a replacement name is nevertheless required for the Reuss species (P.K. Tubbs, ICZN, pers comm. September 1990). This not only avoids potential problems should the synonymy between *R. tuberosa* and *R. sarthacensis* be rejected sometime in the future, but also prevents possible confusion between the species of Reuss and the name of the valid type species of *Reptomultelea*.



Figs 169–172 *Reptomultelea betusora* nom. nov., BMNH BZ 1000 Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground, Etretat, Seine-Maritime, France; 169, autozooids and eleozooids, × 46; 170, autozooidal operculum, × 270; 171, apertures of primary (top left) and intramural (lower centre) eleozooids, × 160; 172, autozooidal aperture, × 225.

Therefore, *betusora* is here proposed as a nom. nov. for the *tuberosa* of Reuss (1874).

The types of *Diastopora acupunctata* Novák, 1877 were not available for study during a visit to the Narodni Museum, Prague during June 1986· However, judging from Novák's figures and Voigt photocards of this material, some of Novák's specimens belong to *Reptomultelea betusora*, at least one to *Reptomultelea sarthacensis* d'Orbigny, and several others cannot be identified with any reasonable confidence.

Diastopora confluens Reuss, 1846 (non Roemer) is placed tentatively in the synonymy of *R. betusora*. According to Prof. E. Voigt (pers comm., February 1987), the type specimen was destroyed in 1956, but a similar specimen exists in the collections of the Naturhistorisches Museum, Vienna (Voigt photocard 8650).

Reptomultelea betusora is characterized by the presence of small eleozooids of the trifoliozooid type. In this respect it resembles *R. tuberculata* (d'Orbigny, 1853) but the latter species has more elongate autozooidal and eleozooidal apertures.

Specimens of *R. betusora* from the Turonian of Sarthe and from the Coniacian of Etretat have rather larger zooids than Upper Cenomanian material; however, the difference is not considered sufficient to warrant species separation. Colonies are often nodular in form, like those of *R. levinseni* sp. nov. (see p. 77) and *R. sarissata* Gregory (p. 94) which also occur in bryozoan-rich chalks of the Seine Maritime.

DISTRIBUTION. Upper Cenomanian (*plenus* Zone) to Coniacian, Czechoslovakia, Germany and France.

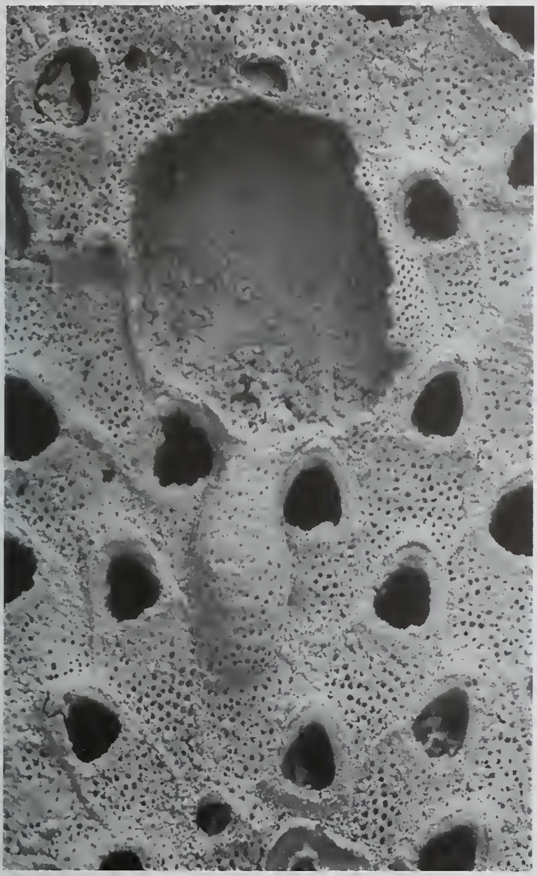


Fig. 173 *Reptomultelea betusora* nom. nov., VH 10436, Upper Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia, gonozooid with broken frontal wall, × 75.

Reptelea bituberosa sp. nov. Figs 174–180

1899 *Reptomultelea tuberosa* d'Orbigny; Gregory: 320, fig. 37.

MATERIAL. Holotype: BMNH 36746, 'Albian, Upper Greensand', Ventnor, Isle of Wight, England, Norman Collection. This specimen comprises one large piece (70 × 45 mm) in matrix, a coated stub with several small fragments, and 7 fragments mounted in two cavity slides. Although the horizon is given as Albian, the close similarity of the matrix to that of a better localized paratype specimen (D58206) from the Isle of Wight suggests that the specimen almost certainly comes from the Lower Cenomanian (*carcitanense* Zone) Glauconitic Marl (formerly known as the Chloritic Marl).

Paratypes: BMNH D44610, 'Upper Greensand' [? Glauconitic Marl], Niton, Isle of Wight, Ford Colln. BMNH D58206 (2 fragments), Lower Cenomanian, *carcitanense* Zone, basal conglomerate of the Glauconitic Marl, Rocken End, Isle of Wight, A. Gale Colln. BMNH D59207, 'Chloritic Marl', St Catherine's Point, Isle of Wight.

NAME. With reference to the two prominent tubercles at either end of the hinge line.

DESCRIPTION. Colony encrusting, multilamellar, characteristically large with up to at least 35 layers, each layer about 0·25 mm in thickness. Overgrowths (Fig. 179) develop by eruptive budding onto the colony surface, often from several closely-spaced pseudoancestrulae; pseudoancestrula aperture about 0·14 mm long by 0·11 mm wide; peri-pseudoancestrular zooids usually autozooids, occasionally eleozooids. Ancestrula not observed. Organization fixed-walled.

Autozooids (Fig. 174) of very large size, frontally elongate, 2–3 × longer than wide, often hexagonal in outline shape, rather elongate and pointed distally; frontal wall occupying about half of the frontal surface, flat or slightly convex with circular pseudopores; zooecial boundary wall moderately raised. Aperture (Fig. 176) large, very longitudinally elongate, about twice as long as wide, attaining maximum width approximately mid-length, moderately rounded distally; apertural rim well-developed, proximally continuous with prominent tubercles paired at either end of the hinge line; apertural shelf broad distally, tapering proximally towards the hinge line; hinge line raised so that plane of aperture slopes downwards in a distal direction, with a short median bar running between two hinge teeth. Operculum (Fig. 175) often preserved in-situ, convex, with a crescent of slit-shaped pseudopores; sclerite impressions visible on sediment/cement infilling zooids. Terminal diaphragms (Fig. 178) sometimes present, flat, located just beneath level of apertural rim. Intramurally budded autozooids (Fig. 177) observed but uncommon; in-situ opercula may occur.

Eleozooids (Figs 179, 180) abundant, scattered; frontal surface about 2–3 × longer than wide, significantly longer and a little wider than an autozooid; frontal wall occupying less than half of the frontal surface, with circular pseudopores present in a similar density to an autozooid. Aperture elongate, over twice as long as wide, widest at the hinge line, initially tapering rapidly and then becoming parallel-sided or slightly spatulate, well-rounded distally; rostrum forming an extensive platform extending beyond distal end of operculum; apertural rim less prominent than that of an autozooid, tubercles absent; hinge line with a wide median bar. Opercula (Fig. 180) often preserved in-situ, surface convex with a crescent of slit-shaped pseudopores; distal end of closed operculum depressed well beneath level of apertural rim; sclerite impressions visible on sediment/cement infilling zooids. Intramurally budded eleozooids and autozooids observed.

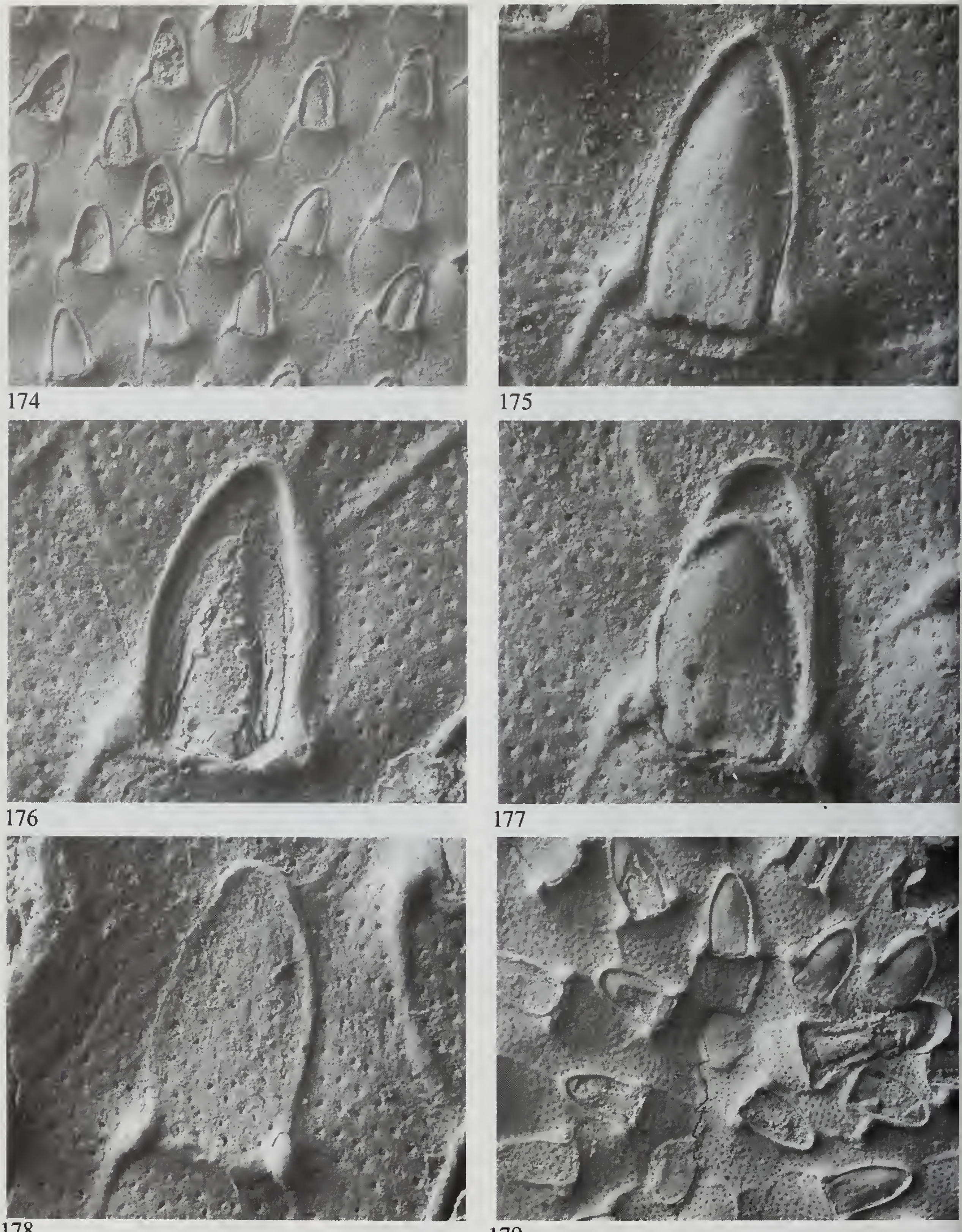
Kenozooids (Fig. 174) developed in moderate numbers, scattered among the autozooids.

Gonozooids present only in the holotype which has two examples, both occurring in areas of overgrowth anastomosis and distorted. Frontal wall about twice as long as wide, with a parallel-sided portion emerging from the maternal aperture, pear-shaped distally. Ooeciopore poorly-preserved in one gonozooid, absent in the second.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype BMNH 36746)

frontal length:	mean = 0.78 mm; SD = 0·069 mm; CV = 8·9; range = 0·65–0·89 mm
frontal width:	mean = 0·32 mm; SD = 0·038 mm; CV = 12·1; range = 0·26–0·38 mm
apertural length:	mean = 0·31 mm; SD = 0·016 mm; CV = 5·1; range = 0·29–0·35 mm



Figs 174–179 *Reptomultelea bituberosa* sp. nov., BMNH 36746, holotype, 'Albian, Upper Greensand' [probably Lower Cenomanian Glauconitic Marl], Ventnor, Isle of Wight, England; 174, autozooids and kenozooids, × 35; 175, autozooidal operculum, × 150; 176, autozooidal aperture with sediment mould of inner surface of operculum, × 150; 177, operculum of intramural autozooid, × 150; 178, autozooidal aperture closed by pseudoporous terminal diaphragm, × 150; 179, overgrowth origin including peri-pseudoancestrular eleozooid, × 50.

apertural width: mean = 0·16 mm; SD = 0·010 mm; CV = 6·7; range = 0·15–0·18 mm

eleozooids (8 zooids from holotype BMNH 36746)
frontal length: mean = 0·92 mm; SD = 0·065 mm; CV = 7·0; range = 0·83–1·00 mm
frontal width: mean = 0·36 mm; SD = 0·060 mm; CV = 16·7; range = 0·30–0·50 mm
apertural length: mean = 0·54 mm; SD = 0·044 mm; CV = 8·1; range = 0·48–0·60 mm
apertural width: mean = 0·24 mm; SD = 0·029 mm; CV = 12·0; range = 0·21–0·29 mm

gonozooid (one zooid from holotype BMNH 36746)
frontal length: 2·61 mm
distal frontal wall length: 2·34 mm
frontal wall width: 1·28 mm

REMARKS. Gregory (1899) incorrectly attributed the holotype specimen of this new species to *Reptomultelea tuberosa* d'Orbigny, 1853, a subjective junior synonym of *Reptomultelea sarthacensis* (d'Orbigny, 1851) which is distinguished by the more acute eleozooids (see p. 51). Furthermore, *R. bituberosa* differs from *R. sarthacensis* and other species of *Reptomultelea* in having prominent tubercles at either end of the hinge line in autozooids, and autozooid apertures which are extremely elongate, about twice as long as wide.

Fig. 180 *Reptomultelea bituberosa* sp. nov., BMNH 36746, holotype, 'Albian, Upper Greensand' [probably Lower Cenomanian Glauconitic Marl], Ventnor, Isle of Wight, England; secondary electron image of coated specimen showing eleozooid with in-situ operculum, × 130.

DISTRIBUTION. Lower Cenomanian, Glauconitic Marl (*carcitanense* Zone) of the Isle of Wight.

Reptomultelea canui (Voigt, 1924) Figs 181–183, 185–190

1924 *Semimultelea canui* Voigt: 167, pl. 4, figs 12–13.

MATERIAL. Type: Although the type material of this species was destroyed during World War 2, the unequivocal identity of the species means that it is not necessary to select a neotype.

Other material: BMNH D39514, D39518 (2 pieces), Santonian, Gr. Bülten, Peine, Westfalia, Germany. VH 10305, Lower Santonian, Vallstedt, Westfalia, Germany.

DESCRIPTION. Colony multilamellar, each layer about 0·5 mm thick, the basal surface of the colony sometimes growing free from the original substrate of encrustation and incorporating secondary substrates (Figs 181–183). Overgrowth origins depressed; pseudoancestrula an autozooid, an eleozooid or a kenozooid, surrounded by 6–7 radiating buds (presumably produced by intrazooecial fission) initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged in quincunx except where disrupted near overgrowth origins and anastomoses.

Autozooids (Figs 185, 188) of medium size, frontally elongate, almost twice as long as wide, rhomboidal in outline, well-rounded distally; frontal wall gently convex, pseudopores subcircular; boundary wall salient. Aperture (Fig. 187) small, usually longitudinally elongate, up to 1·2 × longer than wide, attaining maximum width about mid-length, well-rounded distally; apertural rim raised, continuous with zooidal boundary wall, thickened and prominent at proximo-lateral corners of apertures; apertural shelf narrow; hinge line bowed. Operculum (Fig. 186) often preserved in-situ (especially in older zooids exposed by exfoliating an overlying layer of zooids), convex; pseudopores radially elongate, arranged in an irregular crescent and numbering about 18–20· Terminal diaphragms (Fig. 187) often present at a level just proximal to the apertural shelf, pseudopores not evident (?absent) in most, abundant in some. Intramurally budded eleozooids common, apertures (Fig. 190) of very similar size and shape to primary eleozooids; intramurally budded autozooids not observed.

Kenozooids infrequent.

Eleozooids (Figs 185, 188) moderately abundant, frontally elongate, about the same length and width as the autozooids but more pointed distally. Aperture (Fig. 189) elongate, about twice as long as wide, narrow arch-shaped, attaining maximum width about mid-length; apertural rim prominent distally. Opercula not observed in-situ. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.
autozooids (10 zooids from VH 10305)
frontal length: mean = 0·58 mm; SD = 0·054 mm; CV = 9·4; range = 0·51–0·71 mm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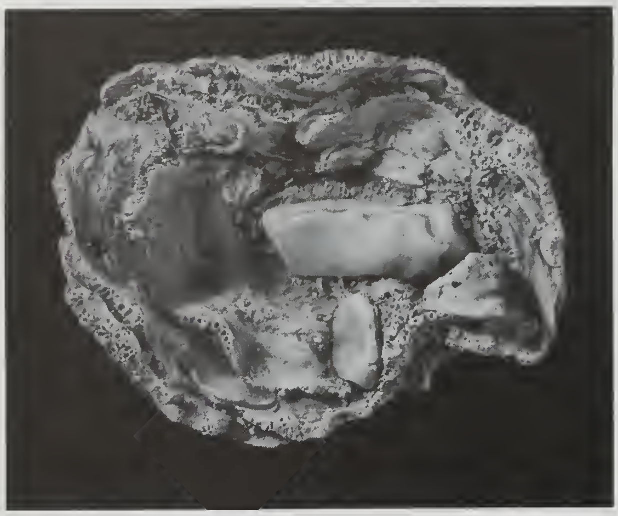
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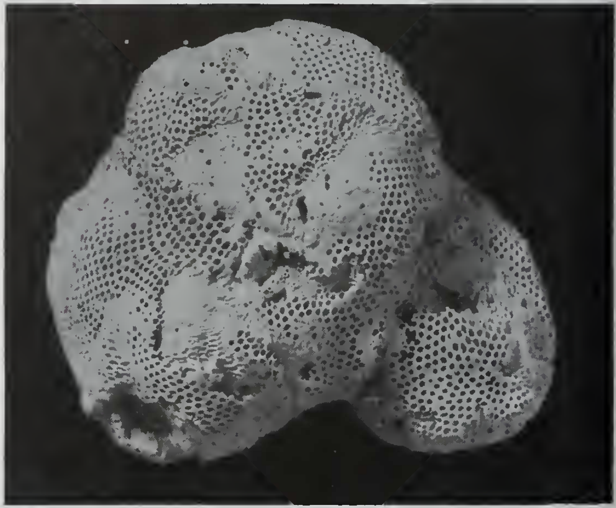
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Figs 181–184 *Reptomultelea* spp., photographs of colonies. 181–183, *R. canui* (Voigt, 1924), VH 10305, Lower Santonian, Vallstedt, Westfalia, Germany, × 2·9; 181, upper side of the colony showing chimney-like growth around an unpreserved object; 182, profile; 183, underside showing original substrate (centre), two secondary substrates (lower right), and free colony growth. 184, *R. goldfussi* sp. nov., EM RE 551.763.31.A745/1, holotype, Cenomanian, Essen, Westfalia, Germany, worn upper surface of colony, × 3·3.

frontal width: mean = 0·30 mm; SD = 0·023 mm; CV = 7·8; range = 0·27–0·32 mm
apertural length: mean = 0·17 mm; SD = 0·010 mm; CV = 6·0; range = 0·15–0·18 mm
apertural width: mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·15–0·17 mm

eleozooids (5 zooids from VH 10305)
frontal length: range = 0·56–0·60 mm
frontal width: range = 0·30–0·33 mm
apertural length: range = 0·12–0·15 mm
apertural width: range = 0·06–0·08 mm

REMARKS. *Reptomultelea canui* co-occurs with the commoner *R. polytaxis* (Voigt, 1924) in the Santonian of Westfalia and can be distinguished from the latter by its larger autozooids and less numerous kenozooids. The combination of well-rounded autozooidal apertures and narrow arch-shaped eleozooidal apertures can be used to recognize *R. canui* among other species of *Reptomultelea*.

DISTRIBUTION. Santonian of Westfalia, Germany.

Reptomultelea convexa sp. nov. Figs 191–196

MATERIAL. Holotype: VH 10467, Turonian (?), Chenu, between Le Mans and Tours, Sarthe, France, collected by G. Breton.

Paratypes: VH 10443, 10444, 10550 (8 fragments), Turonian, Bois de Gareau, near Ecommoi, Sarthe, France.


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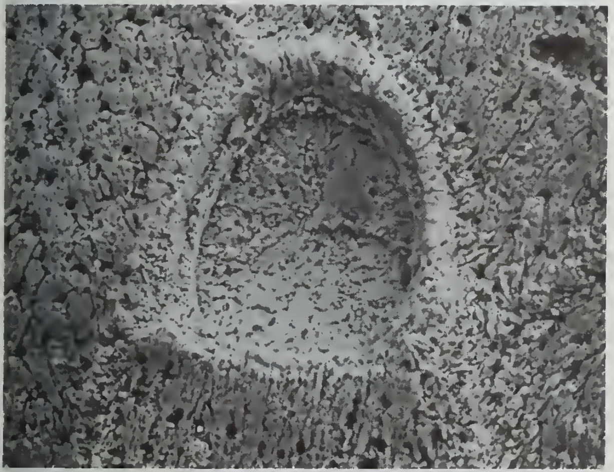
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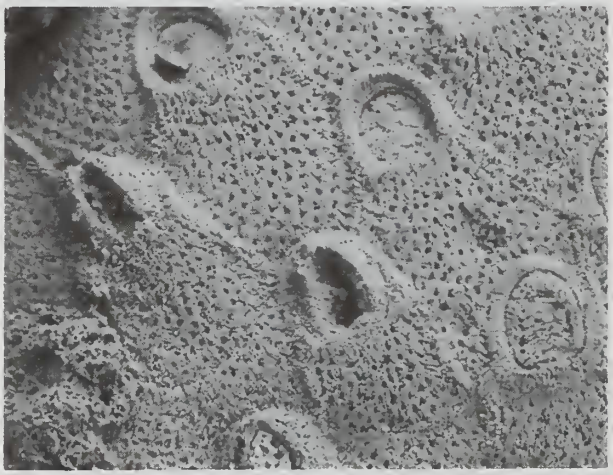
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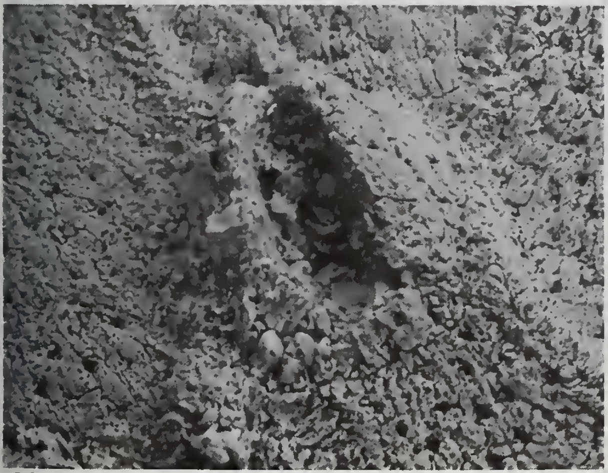
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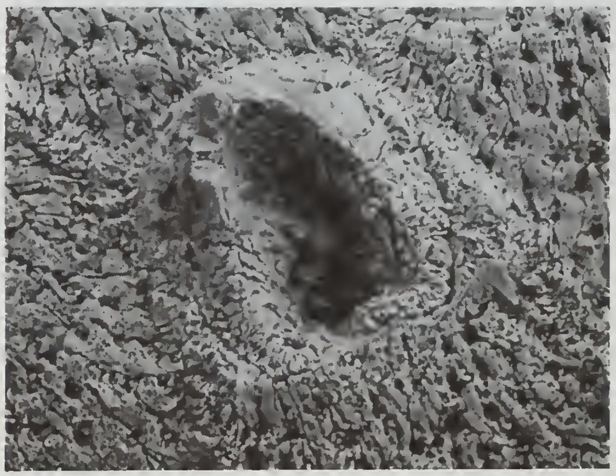
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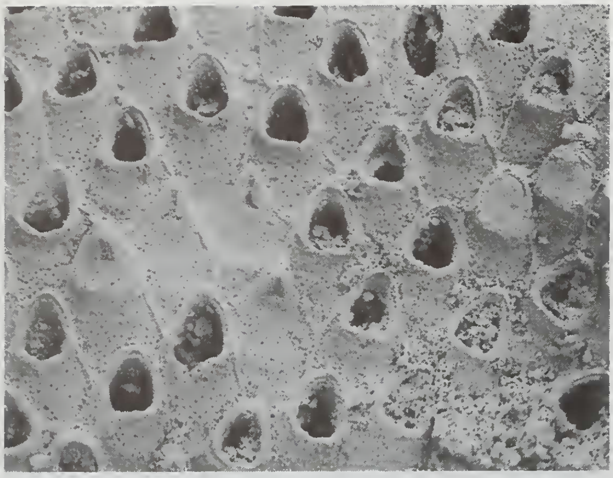
Figs 185–190 *Reptomultelea canui* (Voigt, 1924), VH 10305, Lower Santonian, Vallstedt, Westfalia, Germany; 185, autozooids and eleozooids, × 40; 186, autozooidal operculum, × 300; 187, autozooidal aperture closed by terminal diaphragm, × 250; 188, autozooids and eleozooids, × 85; 189, primary eleozooid aperture, × 250; 190, intramural eleozooid aperture, × 250.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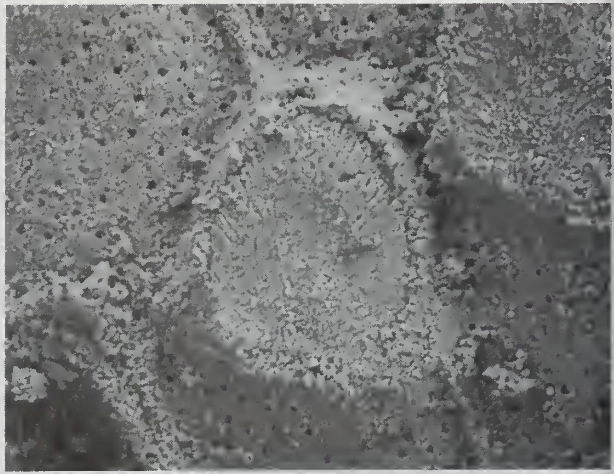
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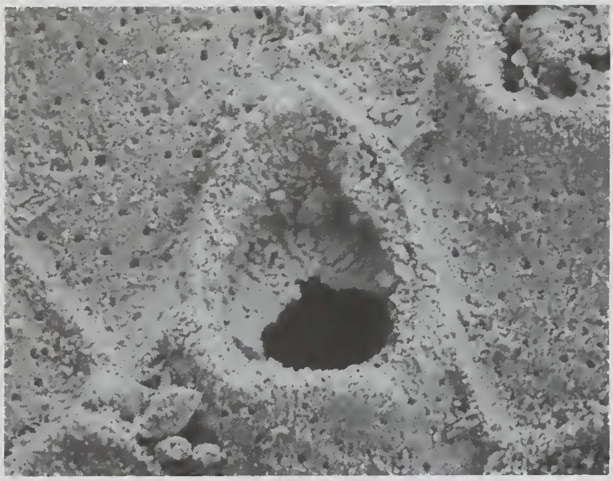
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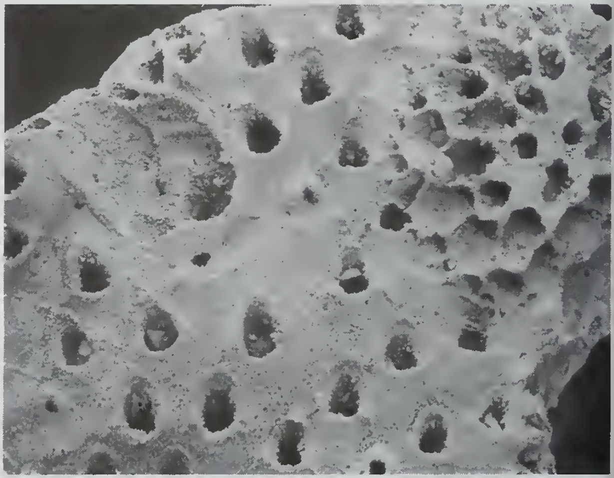
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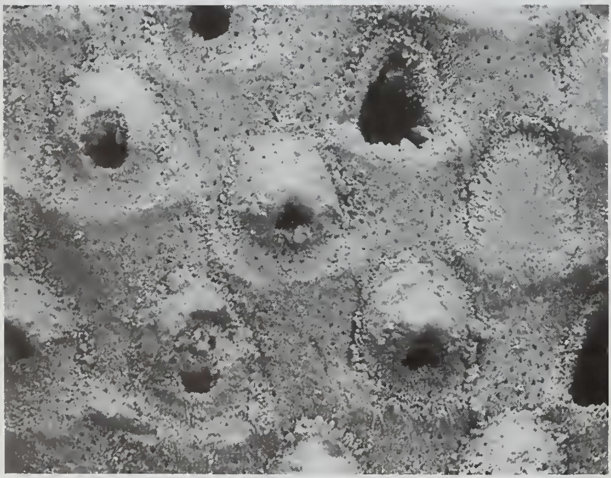
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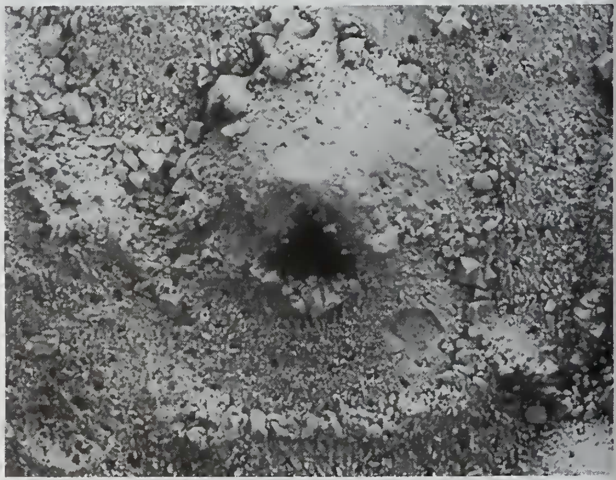
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Figs 191–196 *Reptomultelea convexa* sp. nov. 191–193, VH 10467, holotype, Turonian (?), Chenu, between Le Mans and Tours, Sarthe, France; 191, autozooids and eleozooids, × 42; 192, autozooidal operculum, × 200; 193, autozooidal aperture with broken terminal diaphragm, × 200. 194–196, Turonian, Bois de Gareau, near Ecommoi, Sarthe, France. 194, VH 10444, partly-formed, broken gonozooid (upper left) and overgrowth (upper right), × 33. 195–196, VH 10443; 195, intramural eleozooids and autozooids, × 95; 196, aperture of intramural eleozooid, × 200.

NAME. With reference to the marked convexity of the distal part of the frontal wall.

DESCRIPTION. Colony unilamellar or multilamellar, each layer between 0·23 and 0·30 mm thick, often cavariiform and generally with a free-growing, undulose basal lamina. Overgrowths (Fig. 194) originate through intrazooecial fission. Organization fixed-walled. Apertures arranged roughly in quincunx.

Autozooids (Figs 191, 195) medium-sized, frontally elongate, less than twice as long as wide, usually subhexagonal or subrhomboidal in outline, subrounded distally; frontal wall convex, especially close to the hinge line; boundary wall salient. Aperture (Fig. 193) of moderate size, occupying about a third of the frontal surface, longitudinally elongate, about 1·2–1·3 × longer than wide, arched distally, attaining maximum width about mid-length (or a little proximally of mid-length); apertural rim slightly raised; hinge line poorly preserved in all available specimens; apertural shelf conspicuous, wide to moderately wide, tapering proximally. Operculum (Fig. 192) convex; pseudopores not visible in poorly preserved specimens. Intramurally budded eleozooids common; aperture often cowl-like, directed proximally (Fig. 190).

Kenozooids infrequent.

Eleozooids (Figs 185, 188) common, often clustered in groups of 2 or 3, frontally elongate, less than twice as long as wide and smaller than the autozooids, pointed distally. Aperture (Fig. 189) of small size, trifoliate, about twice as long as wide. Opercula not observed. Intramurally budded eleozooids apparently present, distinguished from 'non-regenerated' eleozooids by proximal inclination of apertural plane.

Gonozooids known from one complete and one broken example (Fig. 194). Frontally of small size, elongate, over twice as long as wide, a parallel-sided tube of variable length emerging from the maternal aperture and dilating into a subcircular distal portion. Ooeciopore transversely elongate, twice as wide as long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids from holotype VH 10467)

frontal length:	mean = 0·55 mm; SD = 0·053 mm; CV = 9·6; range = 0·48–0·62 mm
frontal width:	mean = 0·33 mm; SD = 0·017 mm; CV = 5·0; range = 0·30–0·35 mm
apertural length:	mean = 0·20 mm; SD = 0·009 mm; CV = 4·3; range = 0·18–0·21 mm
apertural width:	mean = 0·16 mm; SD = 0·007 mm; CV = 4·5; range = 0·15–0·17 mm

eleozooids (8 zooids from holotype VH 10467)

frontal length:	mean = 0·49 mm; SD = 0·052 mm; CV = 10·6; range = 0·44–0·57 mm
frontal width:	mean = 0·28 mm; SD = 0·035 mm; CV = 12·4; range = 0·21–0·32 mm
apertural length:	mean = 0·12 mm; SD = 0·019 mm; CV = 16·6; range = 0·09–0·14 mm
apertural width:	mean = 0·06 mm; SD = 0·005 mm; CV = 8·6; range = 0·06–0·08 mm

gonozooids (1 zooid from VH 10550)

frontal length:	1·62 mm
distal frontal wall length:	1·26 mm
frontal width:	0·71 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·15 mm

REMARKS. This species is represented only by fragmentary specimens which are either cavariiform or free-growing lamellar. The high convexity of the distal frontal wall close to the aperture is particularly characteristic. Eleozooids have trifoliate apertures like those of *Reptomultelea betusora* nom. nov., *R. polytaxis* (Voigt) and *R. auris* sp. nov., but *R. convexa* has much larger autozooids than *R. polytaxis* and is distinguished by its convex frontal walls from all three species.

The intramurally budded eleozooids in the paratypes (Figs 194–196) are more strongly cowled, autozooidal apertures larger and their shelves broader than in the holotype (Figs 191–193). These differences are not considered to warrant species level separation, however, until sufficient material is available to assess species variability.

DISTRIBUTION. Turonian of Sarthe, France.

Reptomultelea dixoni (Lang, 1906) Figs 197–201

1899 *Reptomultisparsa rowei* Gregory: 121 (partim) [non pl. 7, fig. 1].
1906 *Semimultelea dixoni* Lang: 64, figs 4 and 12.

MATERIAL. Holotype: BMNH D7845, [Coniacian], *cortestudinarium* Zone, Pit No. 32 of Dibley (1900), opposite the Rose and Crown Inn, Kenley, S. of Croydon, Surrey, England, Withers and Chatwin Collection.

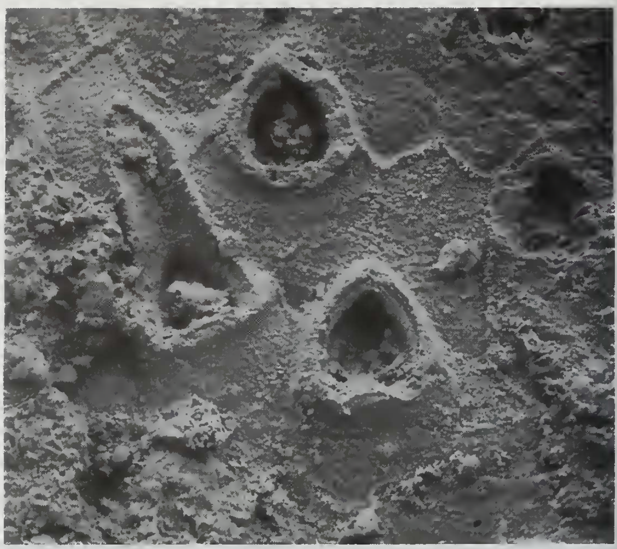
Other material: BMNH D3031 (2 fragments), Upper Chalk, Offham Pit, Lewes, Sussex, Capron Colln (originally described as *Reptomultisparsa rowei* Gregory, 1899). BMNH D31844–50 (fragments of one colony), [Turonian], Dunton Green, Sevenoaks, Kent, England, Dibley Colln. BMNH D43660, [Coniacian], *cortestudinarium* Zone, Seaford Head, Sussex, England, Rowe Colln. BMNH D46061, D46066, Turonian, *lata* Zone, White Cliff to the Hooken, Devon, Rowe Colln. BMNH D57505–9, Coniacian, Craie á *M. normanniae*, above Tilleul No. 3 Hardground (see Kennedy & Juignet, 1974), Etretat, Seine Maritime, France, Taylor & Hammond Colln.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·27–0·41 mm thick, occasionally growing freely with an exposed basal lamina. Overgrowths (Fig. 197) originate through intrazooecial fission from one or several closely-spaced parental zooids; pseudoancestrula either an autozooid (aperture 0·15 × 0·12 mm) or a kenozooid, initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures variably arranged, often irregular.

Autozooids (Figs 198, 199) large, frontally elongate, about 1·6–2 × longer than wide, variable in shape; frontal wall slightly convex, pseudopores apparently small and subcircular; boundary wall salient. Aperture of moderately large size, a little longitudinally elongate, on average 1·1 × longer than wide, attaining maximum width about mid-length, slightly pointed distally; apertural rim raised, drawn to a projecting point distally; apertural shelf narrow, tapering proximally; hinge line short, teeth and bar not clearly visible in the inadequately preserved material available. Operculum (Fig. 200) often preserved in-situ, convex; pseudopores not observed due to poor surface preservation. Terminal diaphragms (Fig. 193) may be present just beneath apertural shelf. Intramural buds not observed.

Kenozooids (Figs 198, 199) common, variable in number, intercalated among other zooids in the normal budding


197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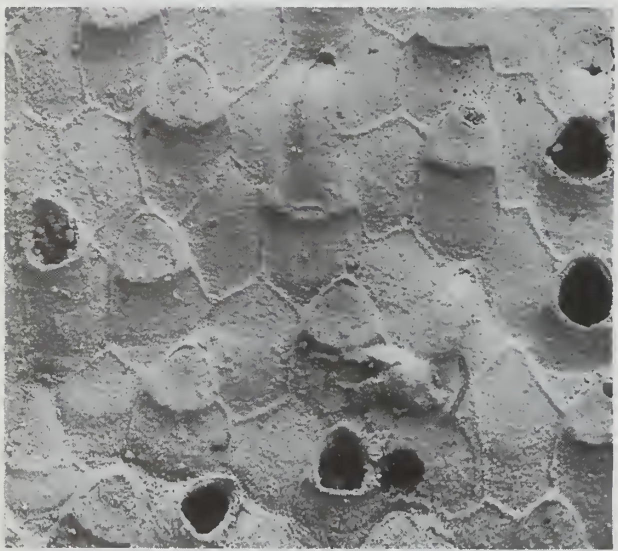
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Figs 197–200 *Reptomultelea dixoni* (Lang, 1906). 197, BMNH D7845, holotype, [Coniacian], *cortestudinarium* Zone, Kenley, Surrey, England, overgrowth origin, × 23. 198, BMNH D31844, [Turonian], Dunton Green, Sevenoaks, Kent, England, autozooids, kenozooids and an eleozooid, × 55. 199–200, BMNH D57506, Coniacian, Craie á *M. normanniae*, Etretat, Seine Maritime, France; 199, autozooids, kenozooids and eleozooids, × 37; 200, autozooidal operculum, × 215.

sequence and also developed at anastomoses between overgrowths; frontally polygonal in outline and invariably shorter and narrower than the autozooids.

Eleozooids (Figs 198, 199, 201) moderately common, frontally elongate, 2–3 × longer than wide, longer but about the same width as the autozooids. Aperture elongate, spatulate, parallel-sided or slightly tapering, widest at the hinge line, rounded distally; rostral shelf extensive, depressed distally. Opercula (Fig. 201) often preserved in-situ; pseudopores not observed due to poor surface preservation. Terminal diaphragms observed. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.
autozooids
(10 zooids from holotype BMNH D7845)

frontal length: mean = 0·73 mm; SD = 0·073 mm; CV = 10·0; range = 0·62–0·84 mm
frontal width: mean = 0·41 mm; SD = 0·050 mm; CV = 12·3; range = 0·36–0·50 mm
apertural length: mean = 0·24 mm; SD = 0·015 mm; CV = 6·3; range = 0·21–0·26 mm
apertural width: mean = 0·22 mm; SD = 0·014 mm; CV = 6·2; range = 0·20–0·24 mm

(5 zooids from BMNH D57506)
frontal length: range = 0·62–0·72 mm
frontal width: range = 0·36–0·41 mm
apertural length: range = 0·23–0·26 mm
apertural width: range = 0·20–0·24 mm

eleozooids (5 zooids from BMNH D57506)

frontal length: range = 0·77–1·05 mm
frontal width: range = 0·32–0·42 mm
apertural length: range = 0·38–0·59 mm
apertural width: range = 0·17–0·29 mm

kenozooids (6 zooids from BMNH D57506)
frontal length: range = 0·48–0·60 mm
frontal width: range = 0·32–0·38 mm

REMARKS. The holotype specimen lacks unequivocal eleozooids, as noted by Lang (1906) in his original description of *Reptomultelea dixoni* which is based entirely on this specimen. However, eleozooids are present in most other colonies (e.g. Figs 198, 199, 201). Among congeneric species, *R. dixoni* closely resembles *R. sarissata* Gregory, 1899 in the morphology of the eleozooid which has an elongate aperture and is often spatulate. However, although similarly pointed, the autozooidal apertures of *R. dixoni* lack the distal prolongations of *R. sarissata* apertures which give them a distinctive ogee arch-shape (Figs 282, 283).

The proportion of kenozooids to other zooids varies greatly between colonies of this species. In some colonies (e.g. BMNH D31844), kenozooids occupy about the same surface area and are more numerous than autozooids. The high proportion of kenozooids in colonies like this one are unrelated to disturbances in growth caused by anastomoses of overgrowths.

Colonies vary from lamellar to nodular in shape. Specimen BMNH D57505 bioimmures a perished substratum of unknown identity which was roughly cylindrical in outline and ornamented by tubercles.

DISTRIBUTION. Turonian (*lata* Zone)-Coniacian (*cortestudinarium* Zone) of southern England and northern France.

Reptomultelea filiozati (Levinsen, 1912) Figs 202–208

1912 *Meliceritites filiozati* Levinsen: 34, pl. 6, figs 7–10.
1990 *Reptelea filiozati* (Levinsen); Taylor: fig. 11.2.

MATERIAL. Lectotype (herein designated): ZMC Levinsen Collection M13, 'Middle Senonian', Fécamp, Seine-Maritime, France; the specimen shown in Levinsen's plate 6, figure 7. Paralectotypes: ZMC Levinsen Colln M12, M14–20, same details as lectotype.

Other material: BMNH D54286–7, Coniacian, Fécamp, Voigt Colln. VH un-numbered specimens from same horizon and locality.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·3 mm thick, often becoming free with a transversely wrinkled basal lamina. Overgrowths apparently originate through intrazooecial fission, often from several closely-spaced pseudoancestrulae (Fig. 206); pseudoancestrulae are autozooids with apertures about 0·11 mm long and wide, sometimes operculate (Fig. 207); peri-pseudoancestrular zooids number 5–6 and commence a zone of secondary astogenetic change marked by increasing zooid size. Organization fixed-walled. Zooidal apertures arranged roughly in quincunx.

Autozooids (Figs 202, 205) of large size, elongate, on average a little less than twice as long as wide, diamond-shaped, pentagonal, rhomboidal or hexagonal in outline, well-rounded distally; frontal wall gently convex, occupying about two-thirds of the frontal surface; pseudopores small, circular; boundary wall salient, clearly visible. Apertures (Fig. 204) of moderate size, elongate, about 1·25 × longer than wide, attaining maximum width about mid-length, well-rounded distally; apertural rim slightly raised; apertural shelf narrow, tapering proximally; hinge line with a median bar. Operculum (Fig. 203) often preserved in-situ, slightly convex; pseudopores not clearly visible in studied material. Diaphragms and intramural buds not observed.

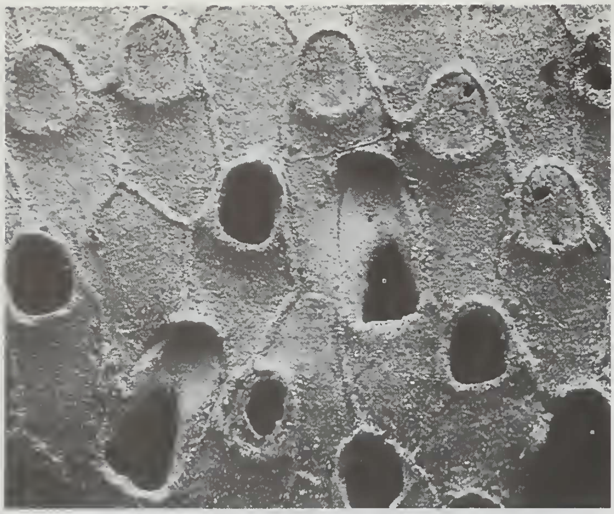
Fig. 201 *Reptomultelea dixoni* (Lang, 1906), BMNH D57505, Coniacian, Craie á *M. normanniae*, Etretat, Seine Maritime, France; eleozooid with in-situ operculum, × 105.

Kenozooids (Figs 202, 205) common, especially clustered at anastomoses between overgrowths.

Eleozooids (Figs 202, 206, 208) moderately common, large, frontally elongate, about 2·5–3 × longer than wide, longer but slightly narrower than the autozooids. Aperture elongate, about twice as long as wide and twice the length of an autozooidal aperture, more or less parallel-sided, well-rounded distally with an extensive rostral platform depressed beneath the level of the apertural rim; hinge line with a long median bar. Opercula not observed in-situ. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.
autozooids (10 zooids from lectotype ZMC M13)
frontal length: mean = 0·62 mm; SD = 0·049 mm; CV = 8·0; range = 0·56–0·71 mm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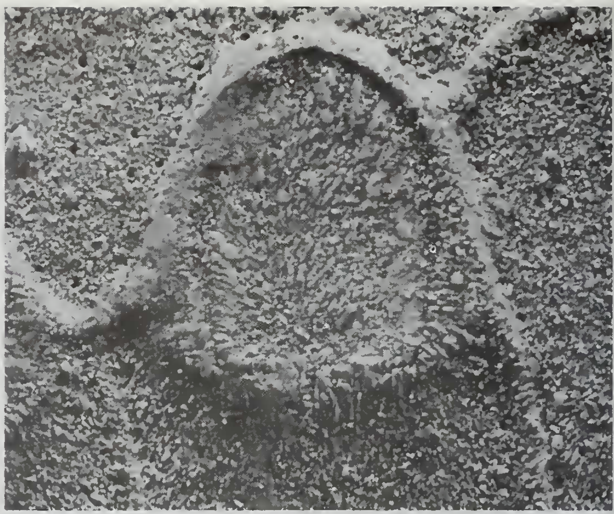
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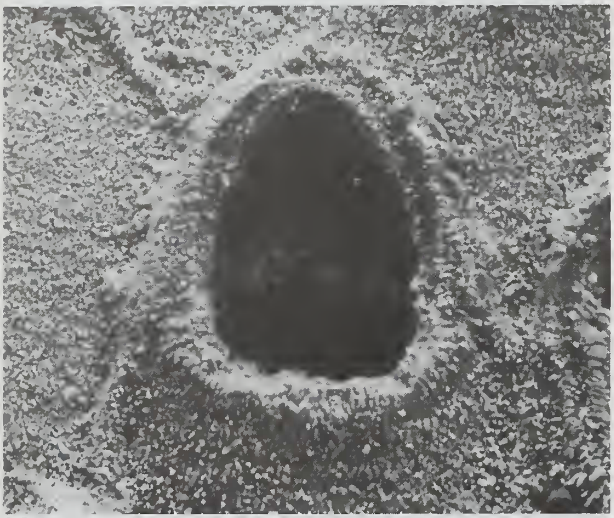
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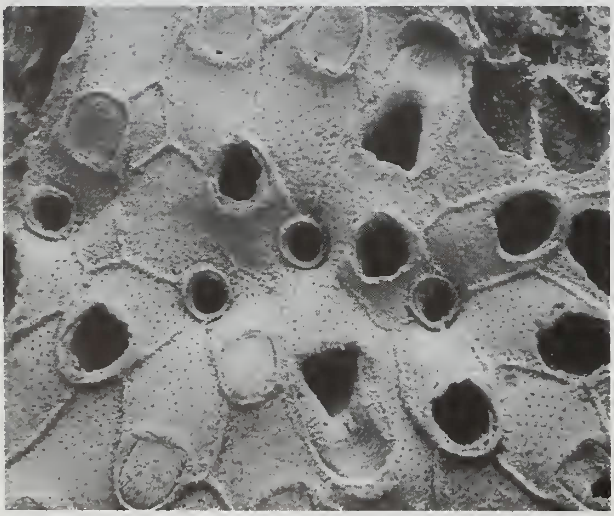
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Figs 202–207 *Reptomultelea filiozati* (Levinsen, 1912), 'Middle Senonian', Fécamp, Seine-Maritime, France. 202–204, ZMC Levinsen Colln M12; 202, autozooids, eleozooids and kenozooids, × 55; 203, autozooidal operculum, × 245; 204, autozooidal aperture, × 250. 205–207, ZMC Levinsen Colln M13, lectotype; 205, area of coalescent growth with kenozooids and autozooids, × 55; 206, four closely-spaced pseudoancestrulae surrounded by radiating autozooids, eleozooids and kenozooids, × 55; 207, operculate pseudoancestrula surrounded by five autozooidal buds, × 78.

Fig. 208 *Reptomultelea filiozati* (Levinsen, 1912), ZMC Levinsen Colln M12, Middle Senonian', Fécamp, Seine-Maritime, France; eleozooid, × 155.

frontal width: mean = 0·34 mm; SD = 0·036 mm; CV = 10·7; range = 0·30–0·42 mm
apertural length: mean = 0·20 mm; SD = 0·009 mm; CV = 4·8; range = 0·18–0·21 mm
apertural width: mean = 0·16 mm; SD = 0·006 mm; CV = 3·9 range = 0·15–0·17 mm

eleozooids (5 zooids from lectotype ZMC M13)
frontal length: range = 0·68–0·80 mm
frontal width: range = 0·27–0·30 mm
apertural length: range = 0·38–0·41 mm
apertural width: range = 0·17–0·20 mm

REMARKS. The shape of the eleozooidal aperture is very characteristic in *Reptomultelea filiozati* and enables immediate distinction from most other species of the genus. Only *R. pegma* sp. nov. (see p. 85) and *R. scanica* sp. nov. (see p. 96) have similarly broad eleozooidal apertures, but both species are readily distinguished from *R. filiozati* by other means (e.g. *R. pegma* has oblique autozooidal apertures with wide apertural shelves, and *R. scanica* has autozooidal apertures which occupy a significantly greater proportion of the frontal surface than in *R. filiozati*).

According to Prof. E. Voigt, this is a rare species. It is known to occur with certainty only in the Coniacian of the Fécamp area of Seine-Maritime in northern France, although the Voigt Collection in Hamburg contains a possible example (un-numbered) from the Coniacian of Villedieu.

DISTRIBUTION. Coniacian of Seine-Maritime, France.

Reptomultelea goldfussi sp. nov. Figs 184, 209–216

MATERIAL. Holotype: EM RE 551.763.31.A745/1, Cenomanian, Essen, Westfalia, Germany. Paratypes: VH 10426, 10548 (8 fragments), Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany.

NAME. In honour of Georg August Goldfuss (1782–1848), the first author to describe a melicerititid species, *Ceriopora gracilis* Goldfuss, 1827, later to become the type species of *Meliceritites* Roemer.

DESCRIPTION. Colony (Figs 184, 211) unilamellar or multilamellar, each layer about 0·25–0·35 mm thick, sometimes growing freely of underlying layers and incorporating secondary substrata. Ancestrula not observed. Overgrowths originate through intrazooecial fission, often from several closely-spaced parent zooids; pseudoancestrula (Figs 212, 213) an autozooid which may be occluded by a terminal diaphragm, initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged in regular quincunx, disrupted close to overgrowth origins.

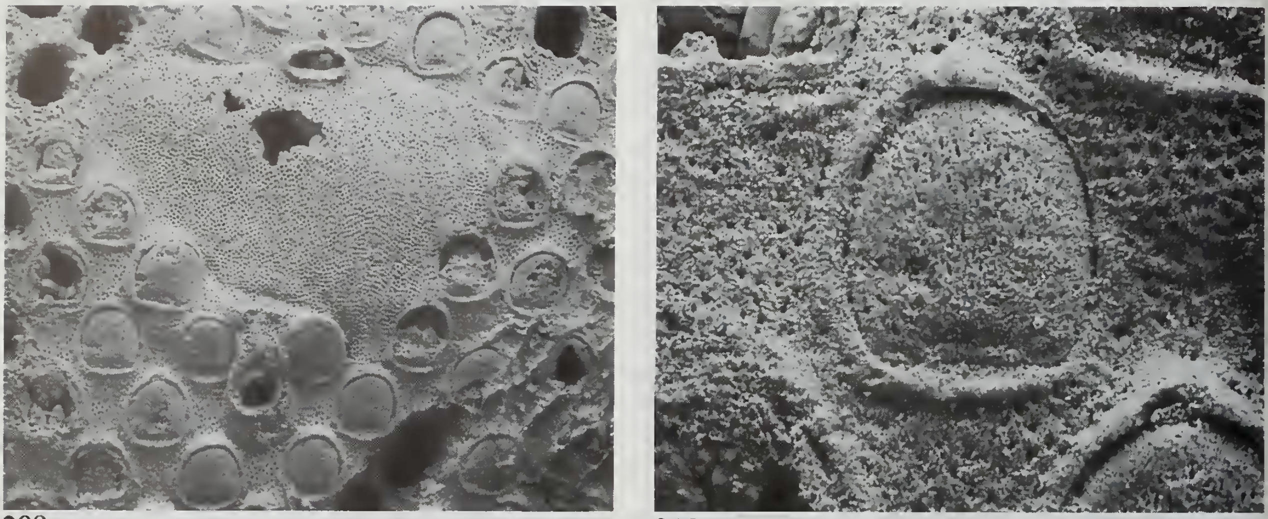
Autozooids (Figs 209, 212) of moderate size, frontally elongate, about 1·5–2 × longer than wide, rhomboidal in outline, well-rounded distally; frontal wall occupying about half of frontal surface, slightly convex, with circular pseudopores; boundary wall salient, variably prominent. Aperture (Fig. 212) large, usually a little longer than wide, attaining maximum width just proximally of mid-length; apertural rim conspicuous but low, continuous with lateral zooecial boundary wall; apertural shelf rather narrow (less than 0·02 mm wide), tapering to nothing at widest point of aperture; hinge line with median bar and low teeth at either end. Operculum (Figs 210, 220) occasionally preserved in-situ, surface convex; pseudopores elongated parallel to growth direction, scattered across entire surface of operculum. Terminal diaphragms seldom observed, pseudoporous. Intramurally budded autozooids uncommon.

Kenozooids not observed.

Eleozooids not observed, presumed absent.

Gonozooids represented by one example in the holotype colony (Fig. 209); frontal surface slightly longer than wide, becoming triangular in outline soon after emergence of the distal frontal wall from the maternal aperture; margins of distal frontal wall irregular, indented by adjacent autozooids. Ooeciopore very large, about the same width as an autozooid aperture but less than half the length.

MEASUREMENTS.
autozooids
(10 zooids with in-situ opercula from holotype EM RE 551.763.31.A745/1)
frontal length: mean = 0·55 mm; SD = 0·051 mm; CV = 9·2; range = 0·48–0·63 mm
frontal width: mean = 0·32 mm; SD = 0·018 mm; CV = 5·5; range = 0·30–0·35 mm


209 210

Figs 209–210 *Reptomultelea goldfussi* sp. nov., EM RE 551.763.31.A745/1, holotype, Cenomanian, Essen, Westfalia, Germany; 209, gonozooid and autozooids, × 30; 210, autozooidal operculum, × 150.

apertural length: mean = 0·26 mm; SD = 0·022 mm; CV = 8·8; range = 0·23–0·30 mm
apertural width: mean = 0·25 mm; SD = 0·018 mm; CV = 7·2; range = 0·23–0·29 mm

gonozooids
(1 zooid from holotype EM RE 551.763.31.A745/1)
frontal length: 2·03 mm
distal frontal wall length: 1·80 mm
frontal width: 1·80 mm
ooeciopore length: 0·11 mm
ooeciopore width: 0·24 mm

REMARKS. The large and well-rounded autozooidal apertures distinguish *Reptomultelea goldfussi* from other species in the genus. As noted below (p. 91), *R. goldfussi* resembles *R. reedi* sp. nov. but is distinguished most convincingly by the occurrence of pseudopores across the entire surface of the operculum rather than in a crescentic row. The holotype (Figs 209, 210) differs from the paratypes (Figs 211–216) in having somewhat taller and larger autozooidal apertures. These differences may be astogenetic in origin because the paratypes comprise zooids close to overgrowth originations and probably within secondary zones of astogenetic change.

DISTRIBUTION. Lower Cenomanian of Westfalia, Germany.

Reptomultelea levinseni sp. nov. Figs 217–223

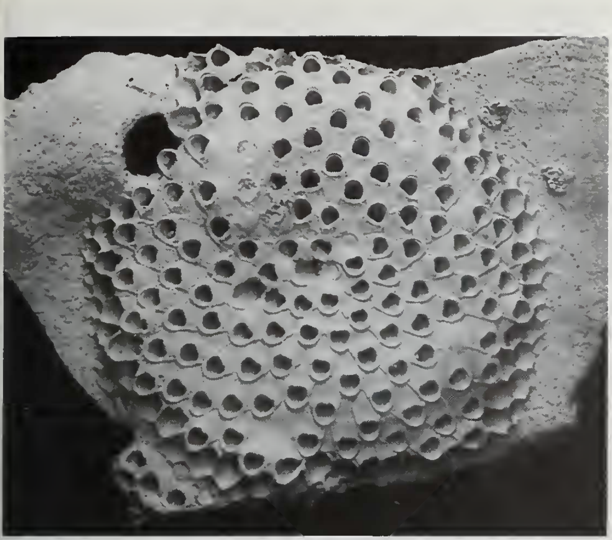
MATERIAL. Holotype: BMNH D58930 (2 fragments), Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine Maritime, France, Taylor & Hammond Collection. Paratypes: BMNH D58931 (sample), D59248, D59249, same horizon and locality as holotype. ZMC Levinsen Colln M56, [?Coniacian], Fécamp, Seine Maritime, France; labelled by Levinsen '*Clausimultelea* sp.n.?'.

NAME. For G.M.R. Levinsen, author of the most important work on melicerititid cyclostomes.

DESCRIPTION. Colony generally multilamellar, each layer about 0·26 mm thick and occasionally growing free of underlying layers and with an undulose basal lamina. Ancestrula not observed. Overgrowths originate by intrazooecial fission, often from several clustered parental zooids depressed beneath general level of colony surface; pseudoancestrula an autozooid or a kenozooid budding a ring of daughter zooids, sometimes including a gonozooid (Fig. 221), forming the initial part of a secondary zone of astogenetic change through which zooid size increases. Organization fixed-walled. Zooids arranged roughly in quincunx.

Autozooids (Figs 217, 218) of large size, frontally elongate, about 2–2·5 × longer than wide, generally hexagonal to diamond-shaped in outline, pointed distally; frontal wall occupying more than half of the frontal surface, slightly convex, with circular pseudopores set in elongate depressions; boundary wall well-defined, salient. Aperture (Fig. 219) of moderate size, approximately 1·5 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width at a point between the hinge line and mid-length; apertural rim well-developed, pointed and raised distally; apertural shelf narrow; hinge line short, with low teeth at either end of a median bar. Operculum (Fig. 220) often preserved in-situ, convex, pseudopores present but number uncertain. terminal diaphragms may be present beneath level of operculum. Intramural buds not observed.

Eleozooids (Figs 217, 218, 223) abundant, scattered; frontal surface about 3–4 × longer than wide, considerably longer than the autozooids but approximately the same width; frontal wall occupying more than half of the frontal surface, slightly convex and with a similar density of pseudopores to the autozooids. Aperture elongate, 2–3·5 × longer than wide, widest a little distally of the hinge line, with a long, narrow rostral area becoming parallel-sided or even very slightly spatulate; rostrum depressed distally; hinge line with a median bar proximal to which is a depressed area; aperture width constricted proximally by wall thickenings which join distally to form the rostral shelf. Operculum (Fig. 223) sometimes preserved in-situ, surface convex, especially distally. Terminal diaphragms and intramural buds not observed.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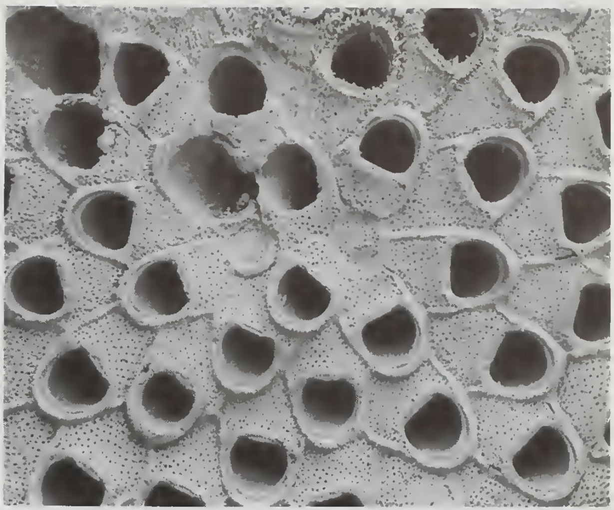
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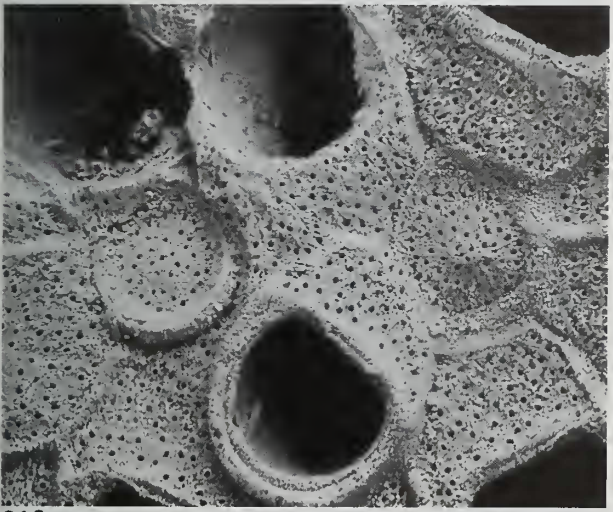
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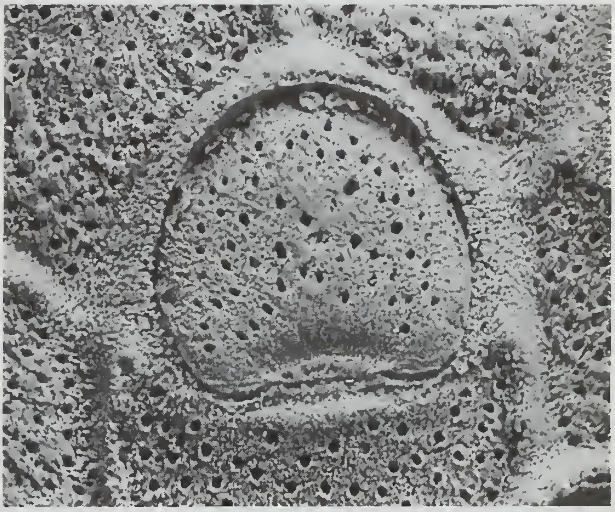
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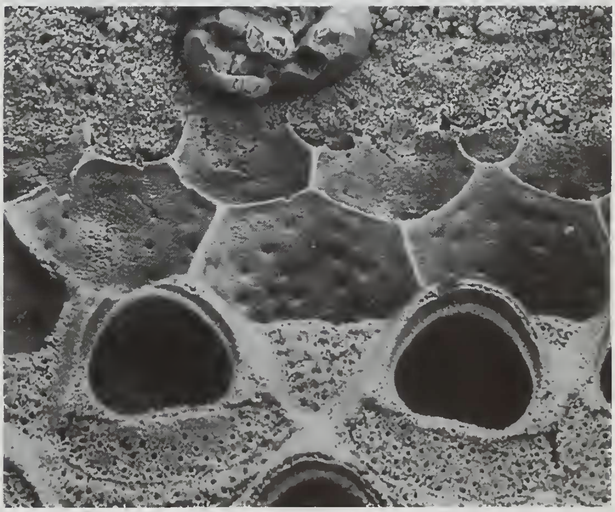
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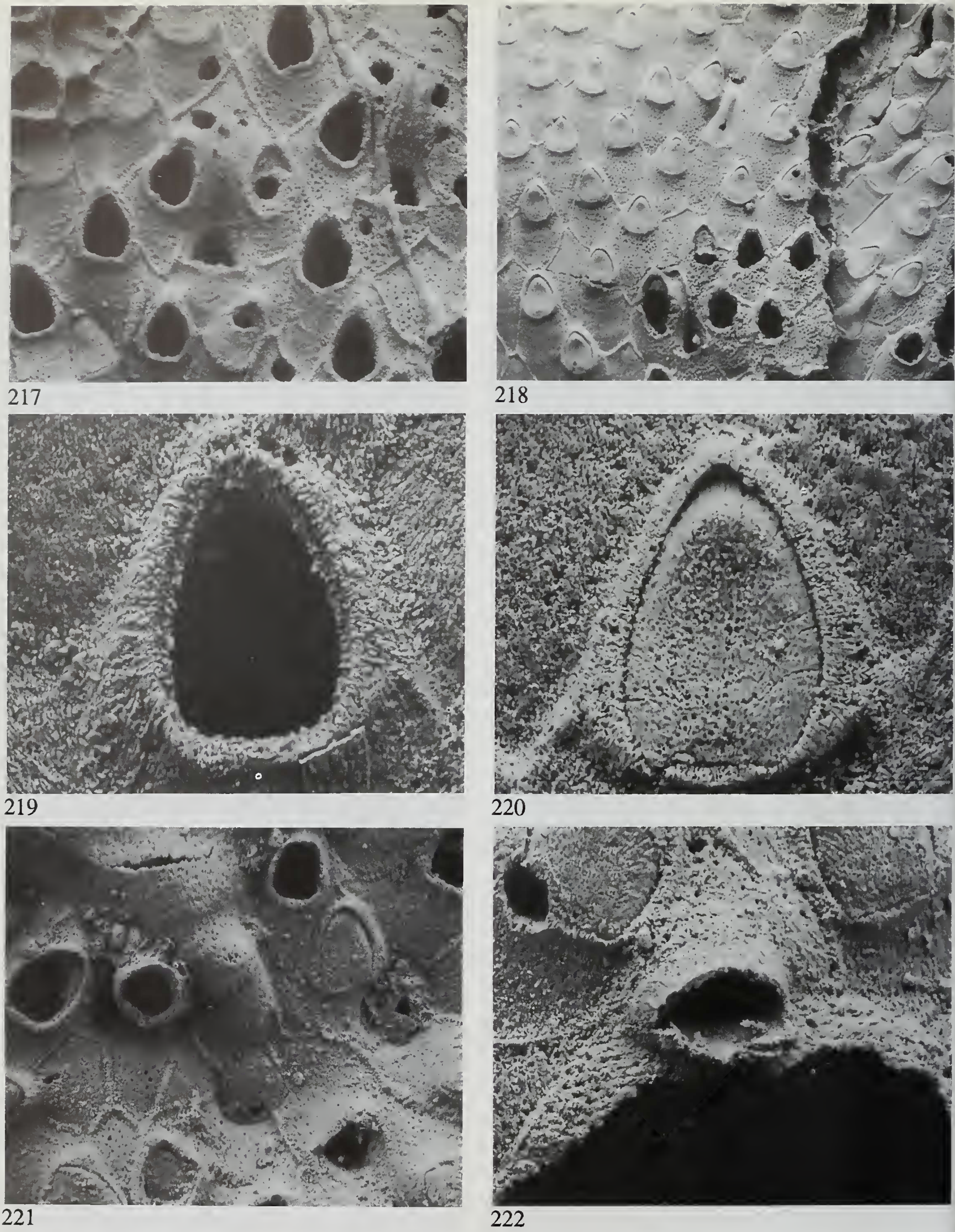
Figs 211–216 *Reptomultelea goldfussi* sp. nov., VH 10426, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 211, small colony encrusting a shell fragment, × 14; 212, autozooids radiating from two closely-spaced pseudoancestrulae with apertures closed by terminal diaphragms, × 45; 213, detail of occluded pseudoancestrulae, × 130; 214, autozooidal operculum, × 200; 215, autozooidal aperture, × 200; 216, growing edge showing new buds with porous interior walls, × 97.



Figs 217–222 *Reptomultelea levinseni* sp. nov. 217, ZMC Levinsen Collection M56, [?Coniacian], Fécamp, Seine Maritime, France; autozooids and two eleozooids with rostra resting on kenozooids, the right-hand eleozooid fouled by a small stomatoporid cyclostome; × 60. 218–222, Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine-Maritime, France. 218–220, BMNH D58930, holotype; 218, partly exfoliated specimen with operculate autozooids and eleozooids, × 28; 219, autozooidal aperture, × 265; 220, autozooidal operculum, × 265. 221, 222, BMNH D59249; 221, gonozooid originating as a first generation bud from a pseudoancestrula (lower centre), × 82; 222, ooeciopore, × 180.

Kenozooids variable in abundance, occasionally isolated but often aggregated, sometimes associated with eleozooids (Fig. 217).

Gonozooids (Fig. 221), known from only one colony (BMNH D52949) which has two, longitudinally elongate, about 1·5 × longer than wide, a short parallel-sided frontal wall emerging from the maternal aperture and dilating to give a subcircular inflated distal frontal wall. Ooeciopore (Fig. 222) transversely elongate. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype BMNH D58930)

frontal length:	mean = 0·66 mm; SD = 0·049 mm; CV = 7·5; range = 0·60–0·75 mm
frontal width:	mean = 0·31 mm; SD = 0·019 mm; CV = 6·2; range = 0·27–0·33 mm
apertural length:	mean = 0·23 mm; SD = 0·008 mm; CV = 3·4; range = 0·23–0·24 mm
apertural width:	mean = 0·16 mm; SD = 0·009 mm; CV = 5·2; range = 0·15–0·18 mm

eleozooids (8 zooids from holotype BMNH D58930)

frontal length:	mean = 1·04 mm; SD = 0·114 mm; CV = 10·9; range = 0·90–1·23 mm
frontal width:	mean = 0·29 mm; SD = 0·014 mm; CV = 4·7; range = 0·27–0·32 mm
apertural length:	mean = 0·52 mm; SD = 0·067 mm; CV = 12·9; range = 0·41–0·60 mm
apertural width:	mean = 0·18 mm; SD = 0·025 mm; CV = 13·6; range = 0·15–0·20 mm

gonozooids (2 zooids from BMNH D52949)

frontal length:	1·70–1·80 mm
frontal width:	1·05–1·20 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·11 mm

REMARKS. This new Coniacian/Santonian species is very similar to *Reptomultelea sarthacensis* from the Cenomanian-?Lower Turonian (see p. 54). The shape and size of the autozooid and eleozooid apertures are indistinguishable in the two species, but *R. levinseni* has autozooids and eleozooids with longer frontal walls, as reflected in the larger frontal length of these zooids (mean values of 0·66 mm for autozooids and 1·04 mm for eleozooids in *R. levinseni* versus 0·48–0·55 mm for autozooids and 0·70–0·81 mm for eleozooids in *R. sarthacensis*).

A notable feature of the only fertile colony available (BMNH D52949) is the budding of gonozooids from pseudoancestrulae, well within secondary zones of astogenetic change. In general, gonozooids in multilamellar melicerititids occur exclusively in zones of astogenetic repetition.

Colonies of *Reptomultelea levinseni* from the *decipiens* Chalk occur as nodular or tube-shaped colonies, the latter having probably grown loosely around organic substrates. *R. sarissata* and other bryozoans from here may adopt similar growth-forms.

DISTRIBUTION. Coniacian and/or basal Santonian, Seine Maritime, France.

Fig. 223 *Reptomultelea levinseni* sp. nov., BMNH D58930, holotype, Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine-Maritime, France; eleozooid with in-situ operculum, × 160.

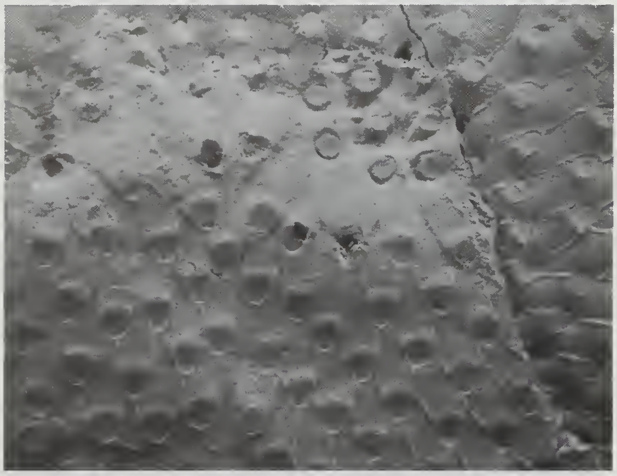
Reptomultelea matutina sp. nov. Figs 224–229

MATERIAL. Holotype: BMNH D52565 (several fragments, including an SEM stub, from one colony), Lower Albian (*tardefurcata-mammillatum* Zones), Shenley Limestone, Munday's Hill Pit, Leighton Buzzard, Bedfordshire, England, R.J. Hogg Collection (see Owen 1972).

NAME. From matutinus, Latin for early (in the morning), with reference to the early geological age of the species.

DESCRIPTION. Colony encrusting, multilamellar (Fig. 224), up to 12 or more layers each about 0·20 mm thick. Ancestrula unknown. Overgrowths develop by eruptive budding onto colony surface from closely-spaced autozooidal pseudoancestrulae located in depressions (Fig. 225); apertures of pseudoancestrulae are smaller and less elongate than those of autozooids from zones of astogenetic repetition, being about 0·15 mm long by 0·14 mm wide.

Autozooids (Fig. 226) of large size; frontally elongate, 2–3 × longer than wide, generally rhomboidal, distally extended and well-rounded by aperture; frontal wall occupying most of the frontal area, convex with circular pseudopores set in elongate depressions; zooecial boundary wall prominent. Aperture small, longitudinally elongate, about 1·2–1·3 × longer than wide, attaining maximum width between the hinge line and mid-length, rounded distally; apertural shelf present; apertural rim well-developed; hinge line with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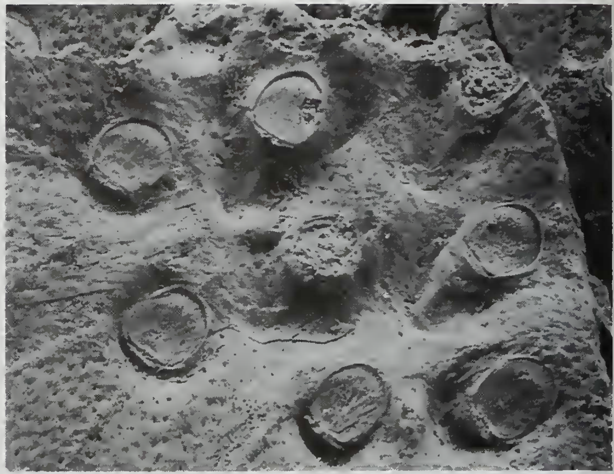
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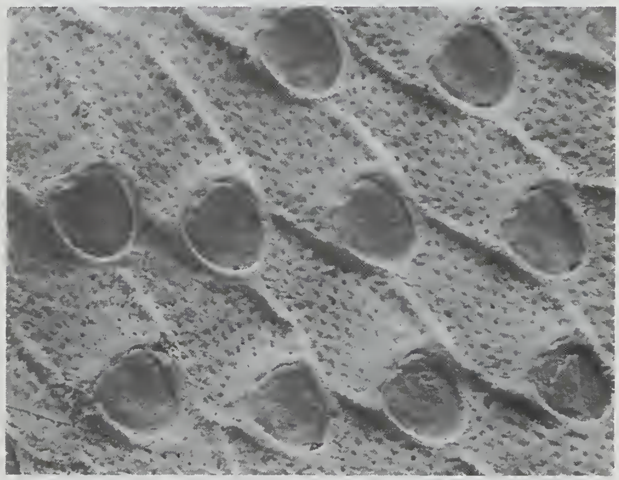
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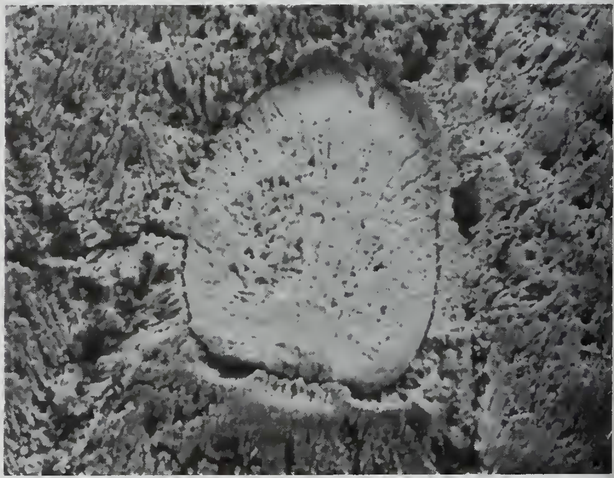
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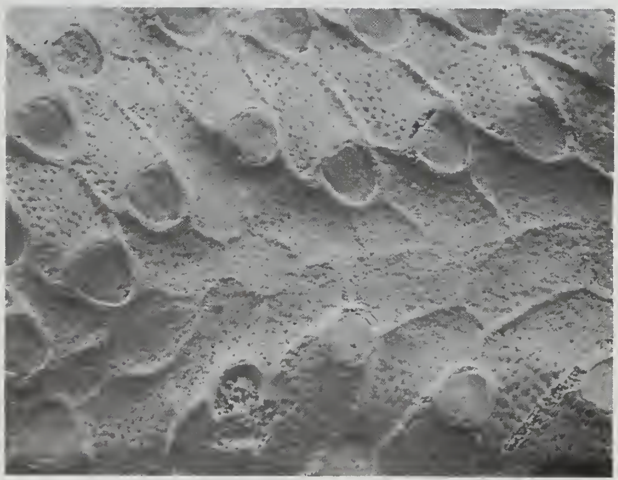
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Figs 224–229 *Reptomultelea matutina* sp. nov., BMNH D52565, holotype, L. Albian (*tardefurcata-mammillatum* Zones), Shenley Limestone, Munday's Hill Pit, Leighton Buzzard, Bedfordshire, England; 224, multilamellar colony with exfoliated layers of autozooids, × 17; 225, depressed area with closely-spaced, operculate pseudoancestrulae, × 60; 226, autozooids growing from top left to bottom right, × 58; 227, autozooidal operculum, × 210; 228, area of coalescent growth, × 41; 229, detail showing kenozooids, × 72.

median bar, raised above general level of frontal surface so that plane of aperture slopes slightly downwards in a distal direction. Operculum (Fig. 227) usually preserved in-situ, surface a little convex, pseudopores apparently absent. Intramural buds and terminal diaphragms not observed.

Eleozooids absent.

Kenozooids (Fig. 229) mainly developed at overgrowth origins and where growing edges from different overgrowths anastomose (Fig. 228), occasionally present elsewhere interspersed among autozooids.

Gonozooids unknown.

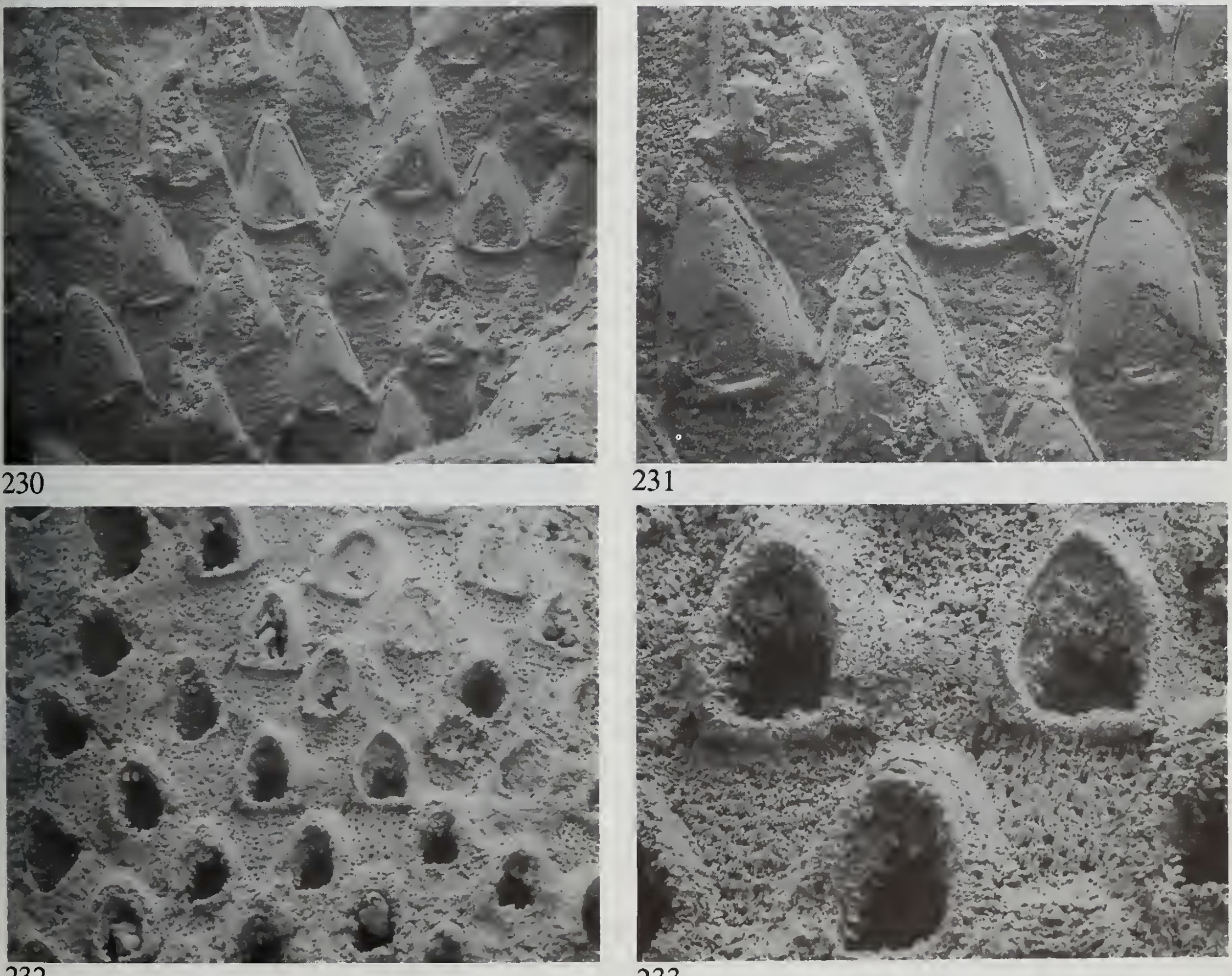
MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype BMNH D52565)
frontal length: mean = 0·72 mm; SD = 0·055 mm; CV = 7·6; range = 0·66–0·81 mm
frontal width: mean = 0·29 mm; SD = 0·019 mm; CV = 6·7; range = 0·26–0·32 mm
apertural length: mean = 0·17 mm; SD = 0·009 mm; CV = 5·6; range = 0·15–0·18 mm
apertural width: mean = 0·13 mm; SD = 0·005 mm; CV = 3·6; range = 0·12–0·14 mm

REMARKS. This is the earliest known species of *Reptomultelea*, and the only species of the genus recorded from the Lower Albian. Only one specimen is known but this is sufficiently different from other species of the genus to warrant recognition as a new species. The absence of eleozooids is best interpreted as a primary characteristic of the species rather than an artefact of small sample size because eleozooids are not developed in areas of anastomosis, where zooid crowding and disruption of the normal budding pattern might be expected to favour their presence. *R. matutina* differs from the somewhat similar *R. oceani* (d'Orbigny) in lacking eleozooids and in having slightly smaller autozooidal apertures.

DISTRIBUTION. Lower Albian of Bedfordshire, England.

Reptomultelea mitrus sp. nov. Figs 230–234

MATERIAL. Holotype: BMNH D14468, Cenomanian [prob-



Figs 230–233 *Reptomultelea mitrus* sp. nov. 230, 231, BMNH D14468, holotype, Cenomanian, Beer Head, Devon, England; 230, operculate autozooids, × 27; 231, detail, × 60. 232, 233, BZ 998, Cenomanian, Wilmington Sands, Grizzle Bed, White Hart Sandpit, Wilmington, Devon; 232, autozooids, × 29; 233, three autozooidal apertures, × 80.

ably Beer Head Limestone Formation, *mantelli* Zone; see Jarvis and Tocher 1987], Beer Head, Devon, England, Bather Collection. Paratype: BZ 998, Cenomanian, Wilmington Sands [a facies of the Beer Head Limestone Fm.], Grizzle Bed, White Hart Sandpit, Wilmington, Devon, Greenaway Colln.

NAME. From Mitra, Latin for head-dress, with reference to the similarity in shape of the operculum to a Bishop's mitre.

DESCRIPTION. Colony multilamellar, each layer about 0·45 mm thick. Ancestrula unknown. Overgrowths arise through intrazooecial fission; pseudoancestrulae are autozooids with apertures about 0·14 × 0·12 mm in size; secondary zones of astogenetic change marked by increasing zooid size and elongation of apertures. Organization fixed-walled. Zooidal apertures closely-spaced, arranged in regular quincunx, disrupted close to overgrowth origins.

Autozooids (Figs 230, 231) of large size, frontally elongate, about 2–3 × longer than wide, typically diamond-shaped in outline but sometimes rhomboidal; frontal wall convex, occupying about half of the frontal surface, with circular pseudopores; boundary wall inconspicuous, slightly salient. Aperture (Fig. 233) very large, elongate, about 1·5 to almost twice as long as wide, attaining maximum width between the hinge line and mid-length, mitre-shaped, pointed distally; apertural rim narrow; apertural shelf narrow, tapering proximally; hinge line with median bar and low teeth at either end. Operculum (Fig. 234) often preserved in-situ, strongly convex; pseudopores elongate, numbering about 20, arranged in an irregular crescent often confined to the proximal half of the operculum. Terminal diaphragms may be present just beneath level of apertural shelf. Intramural buds not observed.

Eleozooids unknown, presumed absent.

Gonozooids not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype BMNH D11468)

frontal length:	mean = 0·73 mm; SD = 0·084 mm; CV = 11·4; range = 0·63–0·86 mm
frontal width:	mean = 0·32 mm; SD = 0·022 mm; CV = 7·0; range = 0·30–0·38 mm
apertural length:	mean = 0·35 mm; SD = 0·024 mm; CV = 6·7; range = 0·32–0·38 mm
apertural width:	mean = 0·21 mm; SD = 0·017 mm; CV = 8·1; range = 0·20–0·24 mm

REMARKS. *Reptomultelea mitrus* is characterized by the large and high apertures which are closely-spaced. There is some resemblance with *R. bituberosa* sp. nov., but the prominent tubercles of *R. bituberosa* are totally absent in *R. mitrus* and eleozooids have not been found in this latter species. Apertures in the paratype specimen (Figs 232, 233) of *R. mitrus* are less longitudinally elongate than in the holotype (Figs 230, 231), but this may be due to proximity to overgrowth origins within secondary zones of astogenetic change. Characteristic of the species are the strongly convex opercula and typically diamond-shaped frontal outlines of the zooids. The most prominent, proximal areas of the opercula are often missing in the holotype following exfoliation of overlying layers of the colony (Figs 230, 234).

Neither the holotype nor the paratype preserve their original substrates which may have been aragonitic shells. The paratype is a 'taco-shaped' colony which apparently grew over the edge of a partly enveloped tabular substratum, possibly a bivalve shell fragment.

DISTRIBUTION. Cenomanian of Devon, England.

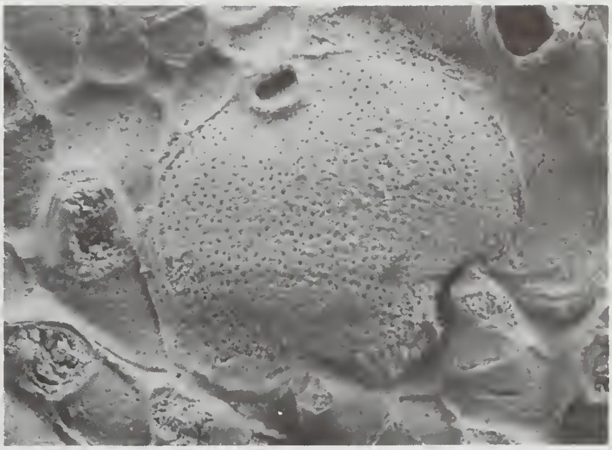
Reptomultelea oceani (d'Orbigny, 1850) Figs 235–242

1850 *Diastopora oceani* d'Orbigny: 176.
1853 *Reptelea oceani* (d'Orbigny); d'Orbigny: 641, pl. 636, figs 5, 6.
non 1872 *Diastopora oceani* (d'Orbigny); Reuss: 110, pl. 27, figs 2, 3.
1890 *Reptelea oceani* (d'Orbigny); Pergens: 399.
1899 *Reptelea pulchella* (d'Orbigny) var. *plana* (d'Orbigny); Gregory: 292 (partim), fig. 31.
non 1899b *Reptelea oceani* (d'Orbigny); Gregory: 295.
1906 *Semimultelea irregularis* d'Orbigny; Lang: 63.
?1906 *Reptelea oceani* (d'Orbigny); Lang: 63.

MATERIAL. Holotype: MNHN d'Orbigny Collection 6561 (Fig. 235) (Voigt photocards 5681 and 5703), Cenomanian, Le Havre; this specimen measures about 24 × 16 mm and is an excellent match with d'Orbigny's figure (1853: pl. 636, figs

Fig. 234 *Reptomultelea mitrus* sp. nov., BMNH D14468, holotype, Cenomanian, Beer Head, Devon, England, autozooidal operculum, × 205.


235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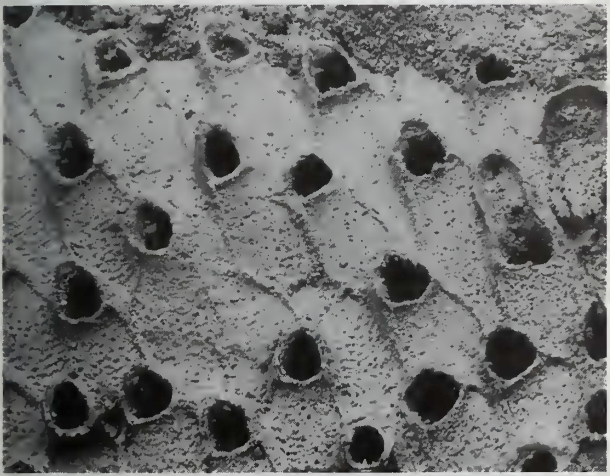
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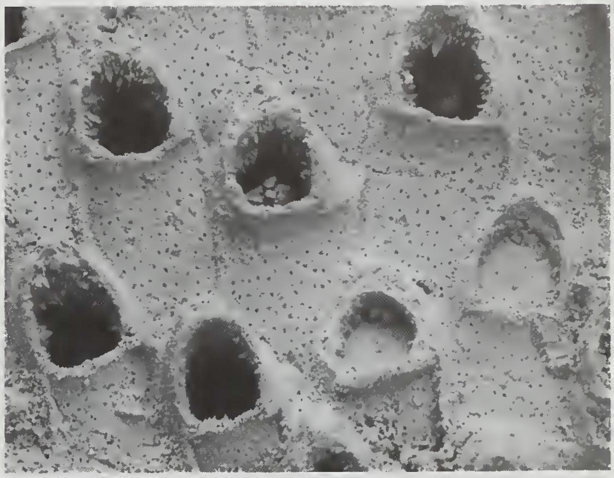
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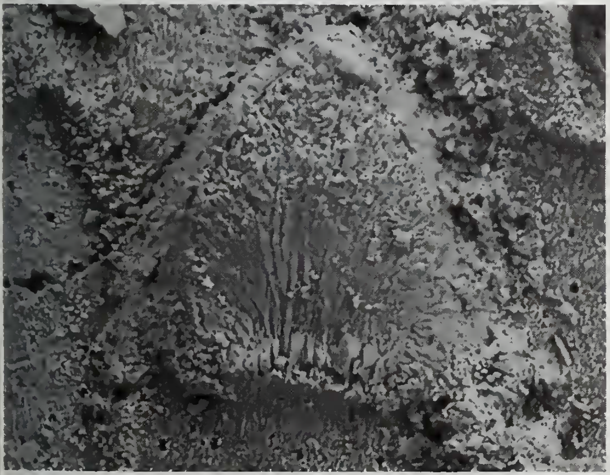
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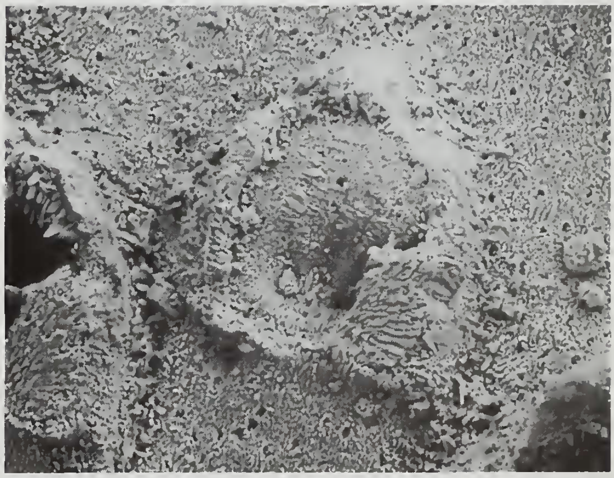
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Figs 235–240 *Reptomultelea oceani* (d'Orbigny, 1850). 235, photograph of MNHN d'Orbigny Collection 6561, holotype, Cenomanian, Le Havre, Seine Maritime, France, × 12. 236, BMNH D4387, Cenomanian, Craie chloritée, Cap de la Hève, Seine Maritime, France, gonozooid with associated autozooids and kenozooids, × 50. 237, BMNH D58737, Cenomanian, Cap de la Hève, autozooids, kenozooids and an eleozooid, × 43. 238–240, VH 10447, Cenomanian, Cap de la Hève; 238, autozooids, the two in the lower right closed by terminal diaphragms with central depressions, × 75; 239, autozooidal operculum, × 215; 240, autozooid with broken operculum and terminal diaphragm beneath, × 198.

5, 6), although the image is reversed in the figure.

Other material: VH 10447, Cenomanian, Cap de la Hève, Seine Maritime, France. VH 10446, Lower Cenomanian, *carcitanensis* Zone, Carrière du Billot, Notre-Dame-de-Fresnaye, Calvados, France, G. Breton Colln. BGS GSM 118079, 118081, 118083, 118085–7, 118103, [Lower Cenomanian], Warminster Greensand, Warminster, Wiltshire, England, purchd from W. Cunnington, 1875. BMNH D7274, [Cenomanian, Warminster Greensand, Warminster], mentd by Lang (1906: p. 63). BMNH D57561–6, Cenomanian, Warminster Greensand, Warminster, J.E. Lee Colln presd 1885. BMNH D59205–6, Upper Albian, Upper Greensand, Chert Beds (about 10 m beneath top), Beer Head, Devon, colld by P.D. Taylor, 1985. BMNH D4387, Cenomanian, Craie chloritée, Cap de la Hève, Seine Maritime, France, figd as *Reptelea pulchella* var. *plana* by Gregory (1899, fig. 31). BMNH D55059–61, Cenomanian, Le Havre, Seine Maritime, France, S. Whiteley Colln. BMNH D58737, Cenomanian, Cap de la Hève, Pitt Colln. BMNH D58899, Lower Cenomanian, Craie Glauconieuse, Cap de la Hève, colld by P.D. Taylor & J. Hammond, 1985. BMNH D58924 (4 pieces), Lower Cenomanian, Craie Glauconieuse, Bruneval, Seine Maritime, colld by P.D. Taylor & J. Hammond, 1985.

Questionably assigned: BMNH D55565, Lower Cenomanian, Glauconitic Marl, Rocken End, Isle of Wight, England, C.W. Wright Colln, 1934.

DESCRIPTION. Colony encrusting, multilamellar (Fig. 235), with layers about 0·3 mm thick. Overgrowths develop by eruptive budding onto the surface of the colony; pseudoancestrula usually an autozooid, chamber continuous with the underlying zooid, which undergoes intrazooecial fission to bud pseudoancestrula and encircling zooids of the overgrowth; zone of secondary astogenetic repetition centred on overgrowths is extensive. Ancestrula not observed. Organization fixed-walled. Autozooids commonly arranged in approximate quincunx.

Autozooids (Figs 237, 238) of large size, frontally elongate, on average 2·5 × longer than wide, irregularly rhomboidal or hexagonal in outline shape, rounded to subrounded distally; frontal wall occupying most of the frontal area, slightly convex with circular pseudopores; zooecial boundary wall prominent but thin. Aperture moderately large, longitudinally elongate, 1·1–1·3 × longer than wide, attaining maximum width about mid-length, moderately rounded; apertural rim well-developed, often pointed distally and elevated so that the plane of the aperture slopes upwards in a distal direction; apertural shelf slight; hinge line bowed, apparently with a median bar. Opercula (Fig. 239) quite often found in-situ, convex, pseudopores not observed. Terminal diaphragms (Fig. 238) sometimes present, generally located well proximal to the apertural rim, in one example underlying a broken operculum (Fig. 240), sparsely pseudoporous and with a central depression and pore. Intramural buds not observed.

Eleozooids (Figs 237, 241, 242) moderately abundant, scattered among autozooids in zones of secondary astogenetic change and repetition; frontal surface large, about 3 × longer than wide, appreciably longer and a little wider than autozooids; frontal wall occupying about half of the frontal surface, pseudopore density not differing from that of autozooids. Aperture elongate, 2–2·5 × longer than wide, slightly spatulate or less often parallel-sided, well-rounded distally; rostrum forming an extensive platform. Terminal diaphragms sometimes present (Fig. 241), occupying a variable proportion of the aperture, sparsely pseudoporous. Opercula not observed. Intramurally budded autozooids may be present in eleozooids (Fig. 242).

Kenozooids especially common in zones of secondary astogenetic change close to overgrowth origins, in areas of anastomosis between overgrowths, and associated with gonozooids (Fig. 236).

Gonozooids (Fig. 236) present in a minority of specimens, although more than 10 examples occur in one moderately-sized colony (VH 10446). Frontal wall equidimensional or up to almost twice as long as wide, with a short parallel-sided portion emerging from the maternal aperture, inflated and densely pseudoporous. Atrial ring present. Ooeciopore transversely elliptical, twice as wide as long, a short and reflexed ooeciostome developed in BMNH D4387.

MEASUREMENTS.

autozooids (10 zooids from VH 10447)

frontal length:	mean = 0·70 mm; SD = 0·066 mm; CV = 9·4; range = 0·62–0·83 mm
frontal width:	mean = 0·28 mm; SD = 0·015 mm; CV = 5·3; range = 0·27–0·32 mm
apertural length:	mean = 0·20 mm; SD = 0·018 mm; CV = 8·6; range = 0·18–0·23 mm
apertural width:	mean = 0·17 mm; SD = 0·014 mm; CV = 8·5; range = 0·15–0·20 mm

eleozooids (10 zooids from VH 10447)

frontal length:	mean = 0·96 mm; SD = 0·081 mm; CV = 8·4; range = 0·86–1·16 mm
frontal width:	mean = 0·32 mm; SD = 0·032 mm; CV = 9·8; range = 0·30–0·41 mm
apertural length:	mean = 0·42 mm; SD = 0·026 mm; CV = 6·3; range = 0·36–0·45 mm
apertural width:	mean = 0·18 mm; SD = 0·010 mm; CV = 5·5; range = 0·17–0·20 mm

gonozooids (8 zooids from VH 10446)

frontal length:	mean = 1·56 mm; SD = 0·219 mm; CV = 14·0; range = 1·29–1·80 mm
distal frontal wall length:	mean = 1·30 mm; SD = 0·204 mm; CV = 15·7; range = 1·07–1·53 mm
frontal width:	mean = 0·91 mm; SD = 0·086 mm; CV = 9·4; range = 0·84–1·05 mm
ooeciopore length:	*ca* 0·06 mm
ooeciopore width:	*ca* 0·12 mm

REMARKS. This species is characterized by its eleozooids with rostra well-rounded distally and spatulate or parallel-sided. Among other species of *Reptomultelea* of similar general morphology, *R. oceani* can be most easily distinguished by the spatulate shape of most of the eleozooid apertures.

Reptomultelea oceani is abundant in the Lower Cenomanian Craie Glauconieuse of Normandy and is also common in the approximately contemporaneous Warminster Greensand of Wiltshire. Specimens from the Warminster Greensand tend to have squatter autozooids than those from the Craie Glauconieuse. A specimen from the Glauconitic Marl (BMNH D55565) is assigned to this species with some reservation because of the distinctly narrower eleozooid aperture and slight differences in autozooid morphology.

DISTRIBUTION. Upper Albian-Lower Cenomanian of SW England and Normandy.

241

242

Figs 241–242 *Reptomultelea oceani* (d'Orbigny, 1850), Cenomanian, Cap de la Hève, Seine Maritime, France. 241, VH 10447, eleozooid with terminal diaphragm, × 115. 242, BMNH D58737, eleozooid containing intramural autozooid, × 112.

Reptomultelea parvula sp. nov. Figs 243–248

MATERIAL. Holotype: VH 10434, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany, Klaumann Colln.

NAME. Parvus, small (L.), with reference to the small size of the zooids.

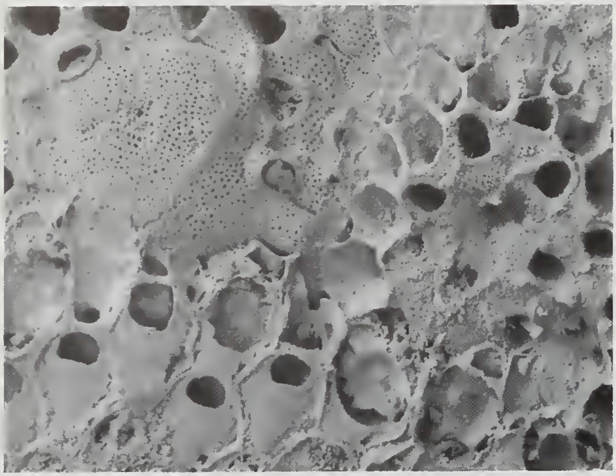
DESCRIPTION. Colony multilamellar with thin layers, each layer about 0·15 mm thick, a transversely folded basal lamina grows free of the bioimmured substratum (?sponge) in the holotype. Ancestrula not observed. Overgrowths (Fig. 243) originate through eruptive budding onto the colony surface (presumably as a result of intrazooecial budding); pseudoancestrula an autozooid with a minute aperture, about 0·09 mm long by 0·06 mm wide, depressed beneath the general level of the colony surface; autozooids in secondary zone of astogenetic change with relatively small, distally rounded apertures; eleozooids in secondary zone of change with short rostra. Organization fixed-walled. Zooids arranged in approximate quincunx.

Autozooids (Figs 245–247) small, frontally elongate, on average slightly over twice as long as wide, typically hexagonal, pointed distally; frontal wall occupying over half of the frontal surface, convex, sparsely pseudoporous; boundary wall well-defined, salient. Aperture (Fig. 248) of small size, on average 1·5 × longer than wide, gothic arch-shaped, attaining maximum width somewhat proximally of mid-length; apertural rim well-developed, prolonged into a tubercle-like structure distally; apertural shelf narrow; hinge bar and teeth not observed. Operculum (Fig. 244) often preserved in-situ, medioproximal surface flat or concave, distolateral edges slightly convex; pseudopores numbering about 16, radially elongate, arranged in a crescent parallel to the distolateral margins. Terminal diaphragms and intramural buds not observed.

Eleozooids (Figs 245–247) very abundant, scattered throughout zones of astogenetic change and repetition; small, frontal surface about 2·5 × longer than wide, similar in width to autozooids but rather longer; frontal wall occupying about half of the frontal surface, sparsely pseudoporous. Aperture elongate, 2–3 × longer than wide, widest close to the hinge line, with a long, narrow rostral area, sometimes very slightly spatulate and rounded distally; apertural rim prolonged into a tubercle-like structure distally. Opercula often preserved in-situ, surface flat proximally, strongly convex in the narrow distal part of the operculum, proximal edge thickened and bowed; pseudopores radially elongate, arranged in a crescent, becoming more widely-spaced distally. Intramural buds not observed.

Gonozooids (Fig. 243) present in the holotype, longitudinally elongate, about twice as long as wide, a variably lengthed parallel-sided portion emerging from the maternal aperture (Fig. 247) and becoming longitudinally ovoidal. Ooeciopore transversely elongate, about twice as wide as long, its proximal edge indented internally by a hemiseptum. Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids from holotype VH 10434)
frontal length: mean = 0·39 mm; SD = 0·033 mm; CV = 8·5; range = 0·35–0·45 mm
frontal width: mean = 0·18 mm; SD = 0·010 mm; CV = 5·5; range = 0·17–0·20 mm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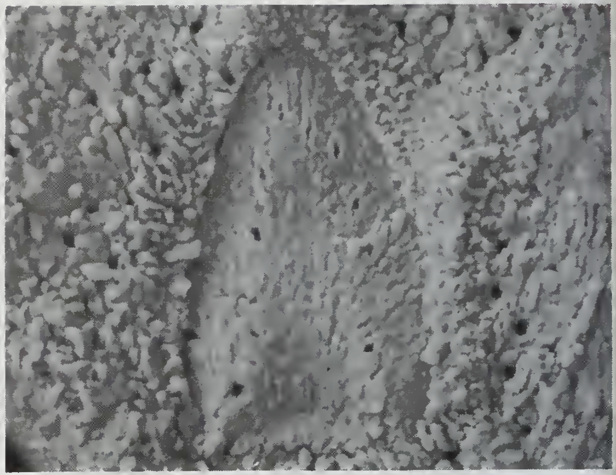
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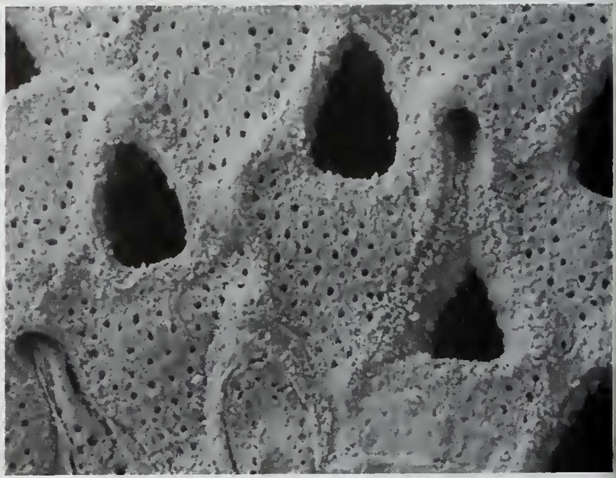
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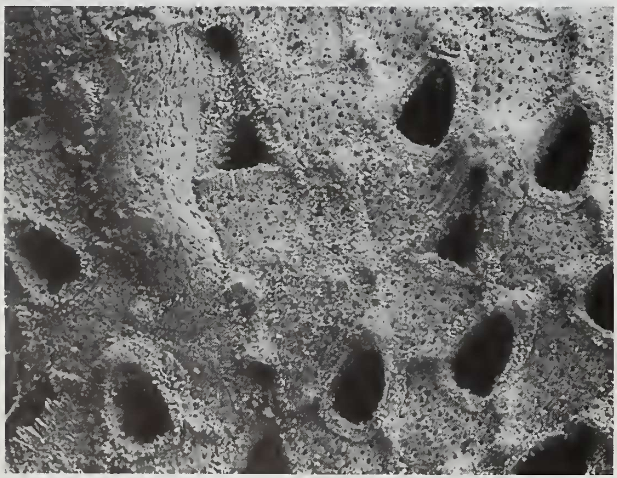
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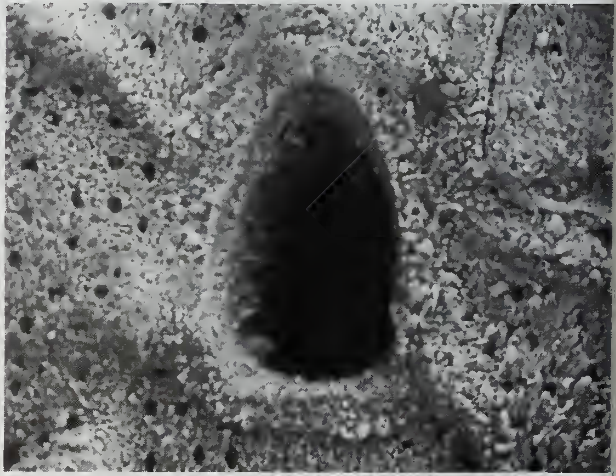
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Figs 243–248 *Reptomultelea parvula* sp. nov., VH 10434, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 243, gonozooid (left), small intrazoarial overgrowth (right), and an overgrowing onychocellid cheilostome (bottom), × 40; 244, autozooidal operculum, × 300; 245, operculate autozooids and three eleozooids, two with in-situ opercula, × 97; 246, autozooids and an eleozooid, × 130; 247, gonozooid origin (left), autozooids and eleozooids, × 85; 248, autozooidal aperture, × 300.

apertural length:	mean = 0·15 mm; SD = 0·010 mm; CV = 6·9; range = 0·14–0·17 mm
apertural width:	mean = 0·10 mm; SD = 0·008 mm; CV = 8·2; range = 0·09–0·11 mm

eleozooids (10 zooids from holotype VH 10434)

frontal length:	mean = 0·45 mm; SD = 0·022 mm; CV = 4·8; range = 0·42–0·48 mm
frontal width:	mean = 0·18 mm; SD = 0·021 mm; CV = 11·5; range = 0·15–0·23 mm
apertural length:	mean = 0·24 mm; SD = 0·017 mm; CV = 6·8; range = 0·23–0·27 mm
apertural width:	mean = 0·09 mm; SD = 0·012 mm; CV = 12·7; range = 0·08–0·12 mm

gonozooids (3 zooids from holotype VH 10434)

frontal length:	1·34 mm (1 zooid)
distal frontal wall length:	0·93–1·14 mm (2 zooids)
frontal width:	0·60–0·68 mm
ooeciopore length:	0·05–0·06 mm
ooeciopore width:	0·11–0·14 mm

REMARKS. This species resembles *Reptomultelea sarthacensis* (d'Orbigny), with which it co-occurs at Mülheim, but has substantially smaller zooids, a difference considered sufficient to warrant its recognition as a new species. Eleozooids seem to be more abundant in *R. parvula* than *R. sarthacensis*, and are present in secondary zones of astogenetic change close to pseudoancestrulae, while autozooidal opercula have a distinct flattened proximal area beyond which is the crescent of pseudopores.

DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Westfalia, Germany.

Reptomultelea pegma sp. nov. Figs 249–255

MATERIAL. Holotype: VH 10430, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. Paratypes: VH 10431, 10543–6, same horizon and locality as holotype.

NAME. Pegma, shelf (L.), with reference to the broad apertural shelf.

DESCRIPTION. Colony unilamellar or locally multilamellar, with each layer about 0·38 mm thick, typically taking the form of a unilamellar expansion with a transversely folded basal lamina indicating growth into free space independent of a substratum. Colony base not observed. Overgrowths apparently originate by intrazooecial fission (Fig. 250) from a group of basal autozooids; later stages not seen. Organization fixed-walled. Zooids arranged in approximate quincunx.

Autozooids (Figs 249, 253) of moderate size, frontally elongate, about 1·5–2 × longer than wide, subhexagonal in outline with a well-rounded distal border and concave proximo-lateral borders; frontal wall occupying much less than half of the frontal surface, very convex with circular pseudopores; zooecial boundary wall generally absent. Aperture (Fig. 251) moderately large, a little longer than wide, attaining maximum width about mid-length, considerably narrower at the proximal edge, well-rounded and strongly depressed distally; apertural rim usually absent but sometimes developed (? signifying intramural budding); apertural shelf very broad, attaining a width of about 0·06 mm distally, tapering proximally; hinge line very short, raised, bowed. Operculum (Fig. 254) often preserved in-situ, convex, with about 20 elongate pseudopores arranged in a crescent extending from either end of the hinge line to mid-length or a little beyond. Terminal diaphragms (Fig. 252) present in a few autozooids slightly beneath the level of the apertural shelf, sparsely pseudoporous. Intramurally budded autozooids not observed, unless occasional autozooids with apertural rims are intramural buds.

Eleozooids (Figs 249, 255) common, scattered; large, frontal surface over 2 × longer than wide, widest near the distal part of the aperture, almost twice the length and 1·5 × the width of an autozooid; frontal wall occupying less than a third of the frontal surface, very convex with circular pseudopores. Aperture elongate, almost twice as long as wide, distinctly spatulate, well-rounded distally; rostrum forming an extensive platform strongly depressed distally; apertural rim absent; hinge line raised, broken in all available specimens. Opercula not observed in-situ. Intramural buds not seen.

Kenozooids occasionally present, sometimes associated with eleozooids.

Gonozooids not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 10430)

frontal length:	mean = 0·48 mm; SD = 0·062 mm; CV = 12·9; range = 0·42–0·63 mm
frontal width:	mean = 0·27 mm; SD = 0·015 mm; CV = 5·6; range = 0·24–0·29 mm
apertural length:	mean = 0·24 mm; SD = 0·019 mm; CV = 8·1; range = 0·23–0·27 mm
apertural width:	mean = 0·23 mm; SD = 0·007 mm; CV = 3·4; range = 0·21–0·24 mm

eleozooids (6 zooids from holotype VH 10430)

frontal length:	mean = 0·82 mm; SD = 0·048 mm; CV = 5·9; range = 0·75–0·89 mm
frontal width:	mean = 0·37 mm; SD = 0·033 mm; CV = 8·8; range = 0·32–0·41 mm
apertural length:	mean = 0·55 mm; SD = 0·039 mm; CV = 7·2; range = 0·51–0·60 mm
apertural width:	mean = 0·31 mm; SD = 0·029 mm; CV = 9·5; range = 0·27–0·36 mm

[nb. apertural length is an estimated value because all available eleozooids have broken hinge lines]

REMARKS. This distinctive new species is notable for the broad apertural shelf, sunken aperture, small frontal wall and short hinge line of the autozooids. The apertural shelf in particular enables a clear distinction to be made from all other species of *Reptomultelea*.

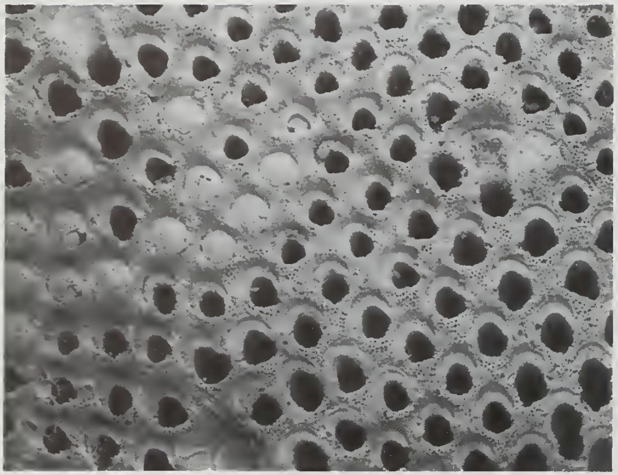
DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Westfalia, Germany.

Reptomultelea polytaxis (Voigt, 1924) Figs 256–262

1924 *Semimultelea polytaxis* Voigt: 166, pl. 4, fig. 11, pl. 5, figs 5, 6.

MATERIAL. The types of this species, originally described from Sudmerberg near Goslar and Gr. Bülten near Peine, Westfalia, were destroyed during World War 2. As the identity of *R. polytaxis* is not in doubt, it would serve no useful purpose to designate a neotype.

Other material: BMNH D31068, D39515–7, D39524, Santonian, Gr. Bülten, Westfalia, Germany, Voigt Colln. VH 10304, 10453, L. Santonian, Gr. Vallstedt, nr Braunschweig,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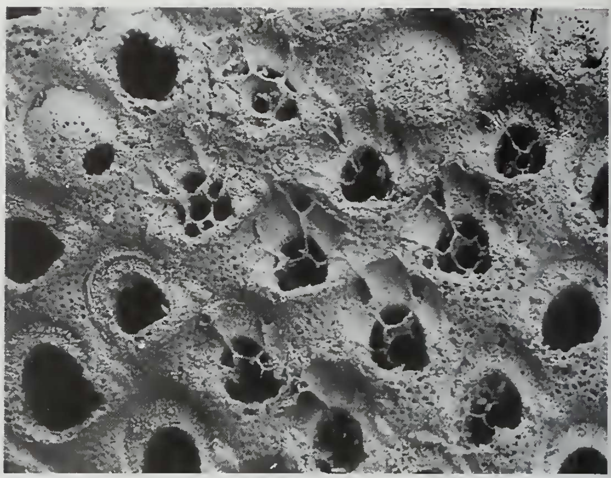
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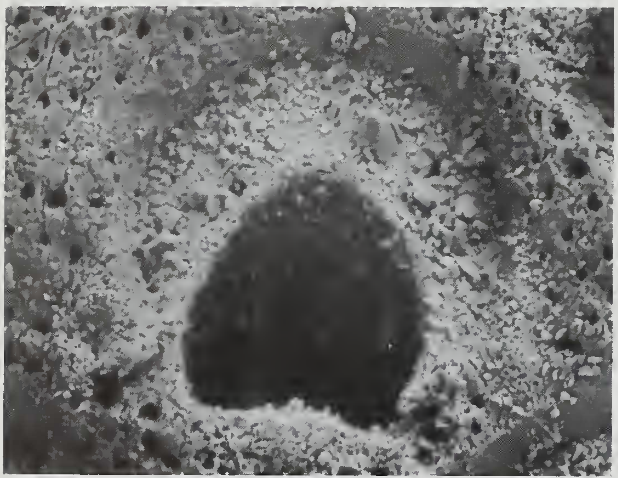
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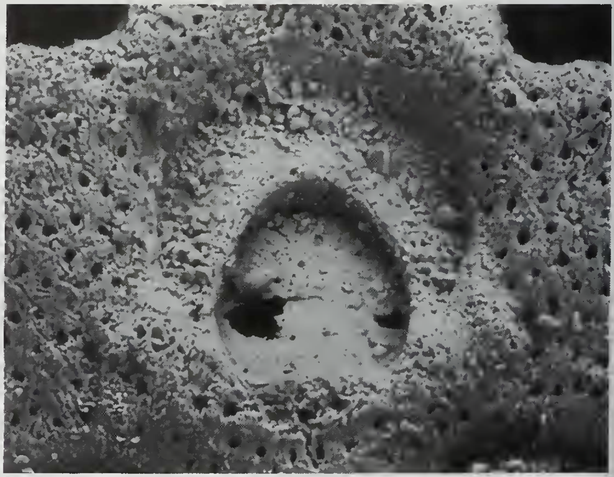
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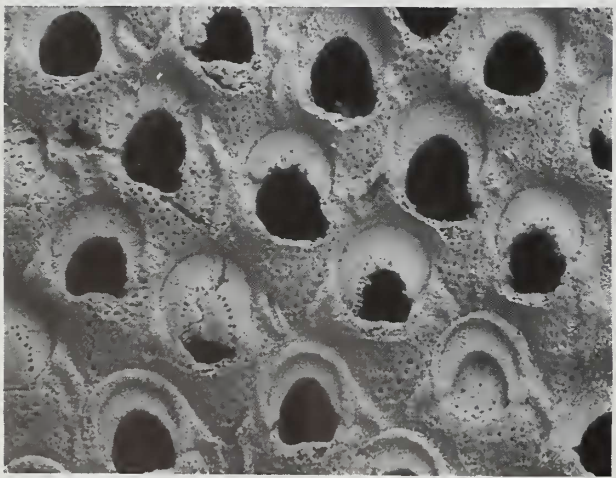
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Figs 249–254 *Reptomultelea pegma* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. 249–252, VH 10430, holotype; 249, autozooids and eleozooids, × 22; 250, autozooids showing intrazooecial fission, × 55; 251, autozooidal aperture, × 270; 252, autozooidal aperture closed by a terminal diaphragm, × 205. 253, 254, VH 10431; 253, autozooids, × 32; 254, autozooidal operculum, × 270.

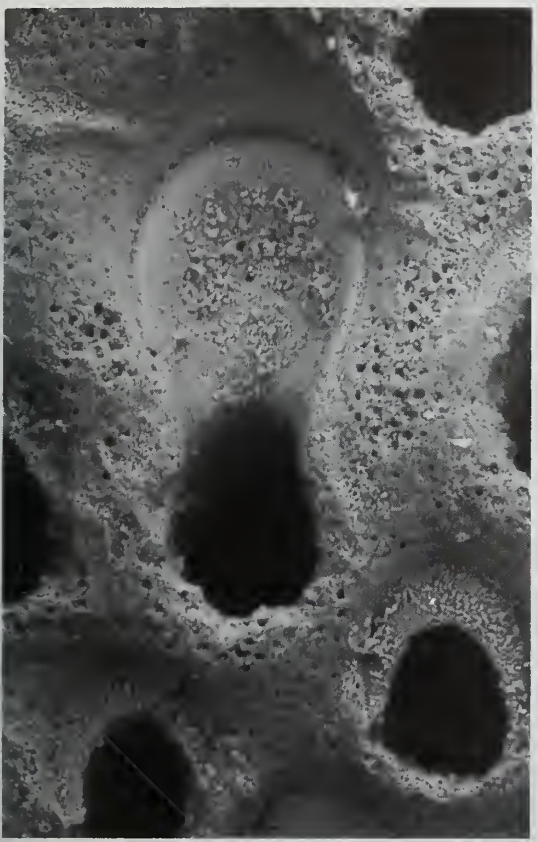

Fig. 255 *Reptomultelea pegma* sp. nov., VH 10430, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; eleozooid with broken hinge line, × 142.

Westfalia, Germany. VH 10440, L. Santonian, Lengede-Broistedt, nr Braunschweig, Westfalia, Germany.

DESCRIPTION. Colony multilamellar, layers variable in thickness from about 0·3–0·5 mm. Basal lamina often growing free of substratum, undulose, when weathered revealing septal trace pattern defining long, narrow basal outlines of zooids (about 0·65 mm long by 0·07 mm wide in VH 10453). Overgrowth origins depressed (Fig. 257), sometimes closely-spaced, originating by intrazooecial fission, the parent zooid forming a central pseudoancestrula surrounded by about 6–7 buds; pseudoancestrula an autozooid or a kenozooid, commencing a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures irregularly arranged, especially close to overgrowth origins and anastomoses.

Autozooids (Figs 256, 260) small, frontally elongate, about twice as long as wide, usually subhexagonal or subrhomboidal in outline, well-rounded distally; frontal wall almost flat, pseudopores subcircular; boundary wall salient. Aperture (Fig. 259) of small size, longitudinally elongate, on average about 1·25 × longer than wide, attaining maximum width between the hinge line and mid-length, well-rounded distally; apertural rim slightly raised; apertural shelf narrow, tapering proximally; hinge line bowed with a short median ridge between hinge teeth. Operculum (Fig. 258) often preserved in-situ, convex; pseudopores numbering about 14, circular or a little elongated radially, arranged in a crescent. Terminal diaphragms occasionally present (SEM-studied examples poorly-preserved). Intramural buds not observed.

Kenozooids (Figs 256, 260) abundant, scattered among the autozooids and eleozooids mostly in zones of astogenetic repetition away from overgrowth origins.

Eleozooids (Fig. 260) abundant, scattered; small, frontally elongate, generally slightly longer than the autozooids but about the same width, tapering distally. Aperture (Fig. 261) small, longitudinally elongate, trifoliate in outline, on average 1·8 × longer than wide and slightly shorter than the autozooidal apertures; however, eleozooids with larger apertures (0·29 × 0·12 mm) are present in VH 10304; apertural rim moderately raised distally. Operculum not observed in-situ. Intramural buds unknown.

Gonozooids (Fig. 262) represented in only one colony. Longitudinally elliptical in frontal outline, the distal frontal wall commencing with a short parallel-sided tube emerging from the maternal aperture. Ooeciopore transversely elongate, about 1·7 × wider than long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from VH 10440)

frontal length:	mean = 0·35 mm; SD = 0·045 mm; CV = 12·9; range = 0·29–0·42 mm
frontal width:	mean = 0·17 mm; SD = 0·016 mm; CV = 9·4; range = 0·15–0·20 mm
apertural length:	mean = 0·15 mm; SD = 0·009 mm; CV = 6·2; range = 0·14–0·17 mm
apertural width:	mean = 0·12 mm; SD = 0·005 mm; CV = 3·9; range = 0·12–0·14 mm

eleozooids (10 zooids from VH 10440)

frontal length:	mean = 0·39 mm; SD = 0·042 mm; CV = 10·8; range = 0·33–0·48 mm
frontal width:	mean = 0·18 mm; SD = 0·017 mm; CV = 9·6; range = 0·15–0·21 mm
apertural length:	mean = 0·14 mm; SD = 0·007 mm; CV = 5·2; range = 0·14–0·15 mm
apertural width:	mean = 0·08 mm; SD = 0·011 mm; CV = 14·4; range = 0·06–0·09 mm

gonozooids (2 zooids from VH 10304)

frontal length:	1·80–1·83 mm
distal frontal wall length:	1·52–1·61 mm
frontal width:	1·04–1·28 mm
ooeciopore length:	0·08–0·09 mm
ooeciopore width:	0·11–0·12 mm

REMARKS. *Reptomultelea polytaxis* can be distinguished from the co-occurring *R. canui* (Voigt) by the smaller size of the autozooidal apertures, the trifoliate eleozooidal apertures, and greater proportion of kenozooids. Among species of *Reptomultelea* with trifoliozooids, *R. polytaxis* differs from *R. tuberculata* (d'Orbigny) in its less elongate autozooidal apertures, and from *R. betusora* nom. nov. in the shorter frontal length of the autozooids, longer eleozooidal apertures, and larger gonozooids. Together with *R. parvula* sp. nov. (p. 82), this has the smallest zooids among species of *Reptomultelea*.

Colonies of *R. polytaxis* may attain large size; VH 10304 has about 14 layers of zooids and measures 78 × 30 mm. This particular colony is rather unusual in having relatively few


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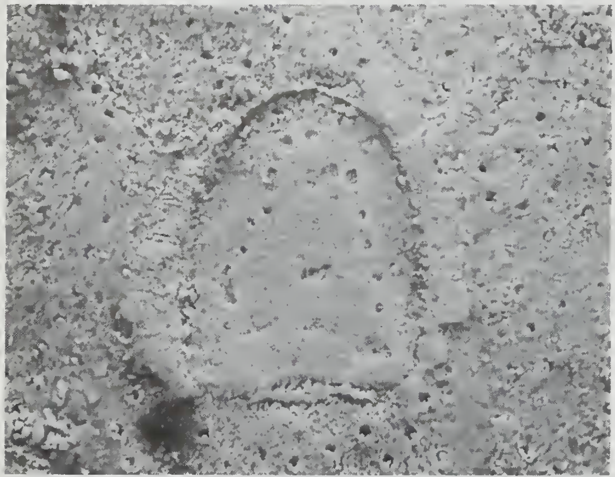
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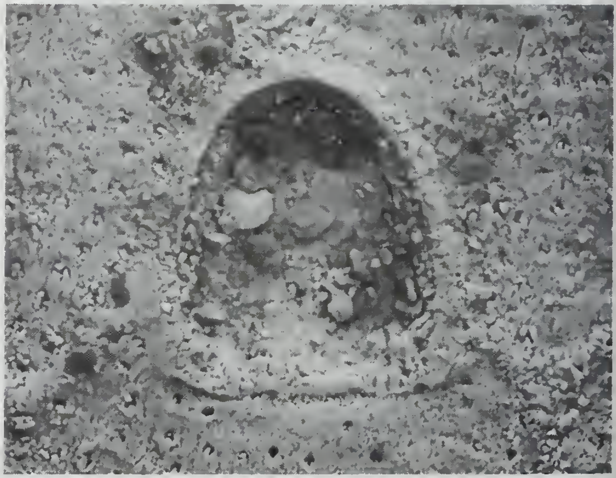
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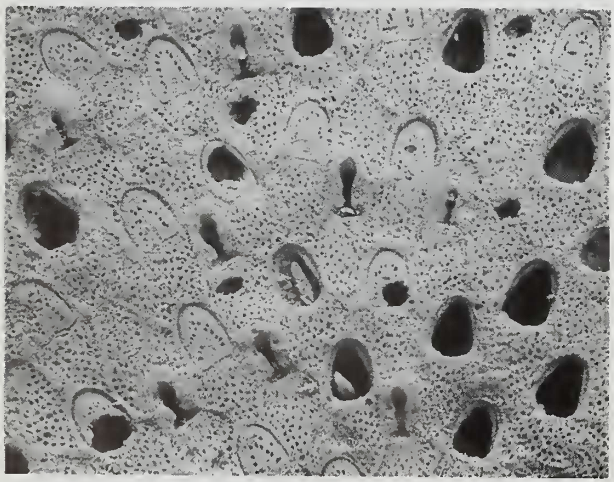
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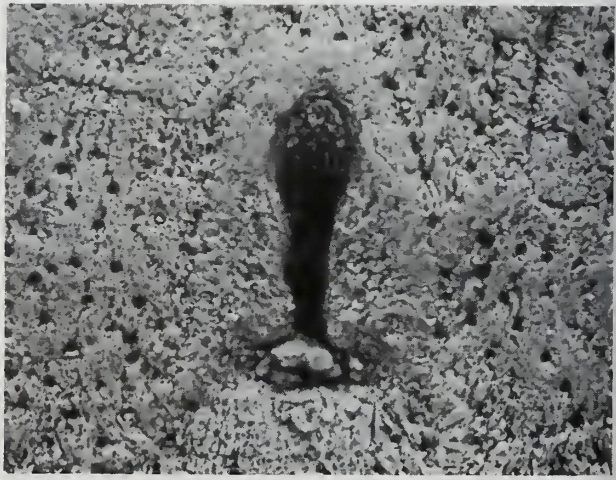
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Figs 256–261 *Reptomultelea polytaxis* (Voigt, 1924). 256–259, VH 10304, L. Santonian, Gr. Vallstedt, nr Braunschweig, Westfalia, Germany; 256, autozooids and kenozooids, × 75; 257, overgrowth origin, × 90; 258, autozooidal operculum, × 300; 259, autozooidal aperture, × 300. 260, 261, VH 10440, L. Santonian, Lengede-Broistedt, nr Braunschweig; 260, autozooids, eleozooids and kenozooids, × 55; 261, eleozooidal aperture, × 300.

Fig. 262 *Reptomultelea polytaxis* (Voigt, 1924), VH 10304, L. Santonian, Gr. Vallstedt, nr Braunschweig, Westfalia, Germany; gonozooid, × 70.

eleozooids which have longer apertures than is typical for the species.

DISTRIBUTION. Santonian of Westfalia, Germany.

Reptomultelea pseudopalpebrosa sp. nov. Figs 263–268

MATERIAL. Holotype: VH 7057, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany, Franke Colln.

NAME. With reference to the similarity of the eleozooids to those of *Meliceritites palpebrosa* Levinsen, 1912.

DESCRIPTION. Colony multilamellar, each layer about 0·4 mm thick. Ancestrula not observed. Overgrowths originate by intrazooecial fission, often from a group of adjacent zooids; pseudoancestrula an autozooid, initiating a zone of secondary astogenetic change of increasing zooid size. Organization fixed-walled. Zooid apertures arranged in approximate quincunx. Frontal walls marked by narrow, slightly sinuous, longitudinal stripes of paler and darker hue.

Autozooids (Figs 263–264) of moderate size, frontally elongate, almost twice as long as wide, often rhomboidal in outline, well-rounded distally; frontal wall occupying more than half of the frontal surface, slightly convex and with circular pseudopores; boundary wall discontinuous, absent along some boundaries but raised into flanges or tubercles elsewhere, especially near the proximo-lateral corners of apertures. Aperture (Fig. 266) moderately large, on average 1·2 × longer than wide, well-rounded distally, attaining maximum width about mid-length; apertural rim absent except in intramural autozooids; apertural shelf broad distally (0·03–0·04 mm), tapering proximally; hinge line with teeth at either end of a median bar. Operculum (Fig. 265) often preserved in-situ, surface convex; pseudopores elongate, arranged in an irregular crescent; sclerites deep (visible as moulds in sediment filling zooecial chambers). Terminal diaphragms present. Intramural autozooids common, differing from primary autozooids in having apertural rims.

Eleozooids common (Figs 263–264), distributed singly or in groups, apparently all intramurally budded and therefore with the same frontal dimensions as autozooids. Apertural area comprises a flat proximal area with few or no pseudopores, a small, D-shaped aperture broader than long and set in an inclined plane directed proximally, and an extensive hood-like distal area (Fig. 268) which is conspicuously pseudoporous, slightly inflated and overlaps the margins of the host aperture. Opercula sometimes in-situ (Fig. 267).

Kenozooids (Figs 263–264) present.

Gonozooids known from a single example, the proximal part of which is obscured. Distal frontal wall subtriangular in outline, broader than long. Ooeciopore transversely elongate, width more than twice the length. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 7057)

frontal length:	mean = 0·49 mm; SD = 0·040 mm; CV = 8·1; range = 0·42–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·020 mm; CV = 7·8; range = 0·23–0·29 mm
apertural length:	mean = 0·21 mm; SD = 0·013 mm; CV = 6·3; range = 0·20–0·23 mm
apertural width:	mean = 0·17 mm; SD = 0·008 mm; CV = 4·5; range = 0·17–0·18 mm

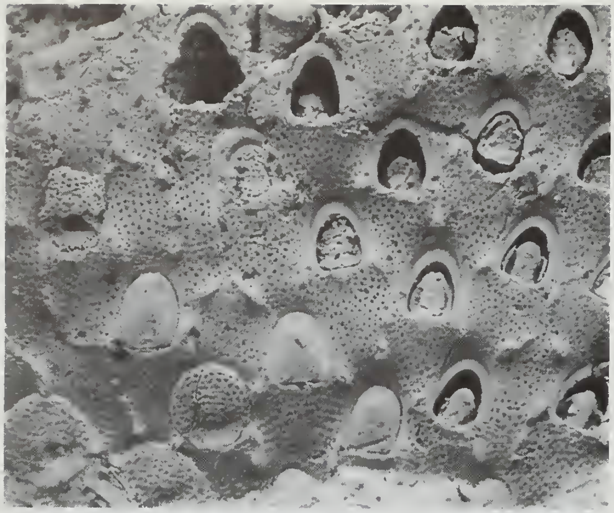
eleozooids (intramural)

apertural length:	*ca* 0·04–0·05 mm
apertural width:	*ca* 0·07 mm

gonozooids (1 zooid from holotype VH 7057)

distal frontal wall length:	1·20 mm
frontal width:	1·56 mm
ooeciopore length:	0·09 mm
ooeciopore width:	0·23 mm

REMARKS. Although known from only a single specimen, a variably-preserved colony 37 × 24 mm in size with at least 17 layers of zooids, this species is sufficiently distinctive to warrant formal naming. No other species of *Reptomultelea* has eleozooids with small semicircular apertures and distal, hood-like areas of pseudoporous calcification. In this aspect, *R. pseudopalpebrosa* most closely resembles *Meliceritites palpebrosa* Levinsen, 1912, a vinculariiform species from the Senonian of France. The apertural shelf is similarly broad in the two species, but the abundant pseudopores distributed over the entire surface of the autozooidal opercula in *M. palpebrosa* differ from those of *R. pseudopalpebrosa*, which are arranged in an irregular crescent. A closer affinity seems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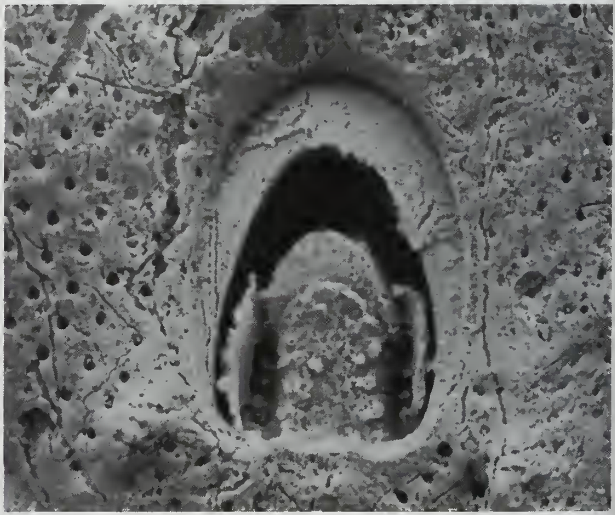
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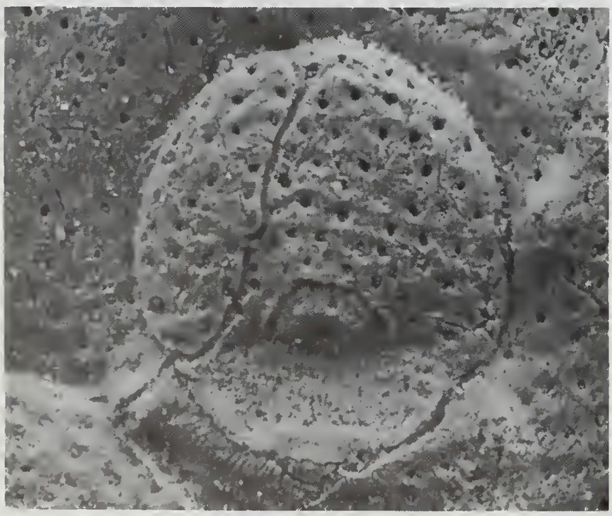
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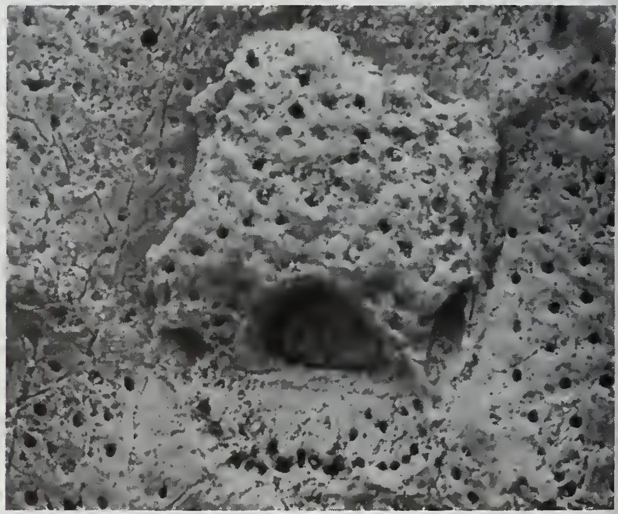
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Figs 263–268 *Reptomultelea pseudopalpebrosa* sp. nov., VH 7057, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 263, autozooids, eleozooids and kenozooids, × 45; 264, operculate autozooids, kenozooids and eleozooids, × 70; 265, autozooidal operculum, × 265; 266, autozooidal aperture partly occupied by sediment mould of the opercular sclerites, × 265; 267, eleozooid with in-situ operculum, × 265; 268, eleozooid aperture and irregular distal hood, × 265.

possible between the two species than is implied by their inclusion in separate genera. The discontinuous, broken zooecial boundary wall visible on the colony surface of *R. pseudopalpebrosa* is another noteworthy feature, as is the occurrence of slightly sinuous longitudinal stripes of alternating lighter and darker calcification on the frontal walls. The origin and significance of these stripes are unknown.

DISTRIBUTION. Lower Cenomanian of Mülheim, Westfalia, Germany.

Reptomultelea reedi sp. nov. Figs 269–274

MATERIAL. Holotype: VH 10429, Upper Cenomanian, St Calais, Sarthe, France.

NAME. In memory of Christopher G. Reed, whose premature death in 1990 curtailed his elegant studies of bryozoan larval morphology and development.

DESCRIPTION. Colony unilamellar, potentially multilamellar (as indicated by presence of incipient intrazooecial budding), layer thickness about 0·45 mm; basal lamina with closely-spaced transverse ridges and grooves. Ancestrula not observed. Intrazooecial fission present, 5 or 6 daughter buds surrounding the chamber of the parental zooid (Figs 271–272). Organization fixed-walled. Zooid apertures arranged in regular quincunx.

Autozooids (Figs 269, 270) of moderate size, frontally elongate, 1·8–2·4 × longer than wide, outline well-rounded distally but indented proximally by apertures of adjacent zooids; frontal wall convex, occupying more than half of the frontal surface, with circular pseudopores; boundary wall subdued salient. Aperture (Fig. 274) small to medium-sized, equidimensional or a little longer than wide, well-rounded distally, attaining maximum width between hinge line and mid-length; apertural rim present, distally most prominent; apertural shelf widest distally (*ca* 0·02 mm), tapering proximally; hinge-line bowed. Operculum (Fig. 273) often preserved in-situ, surface relatively flat with about 16–18 elongate pseudopores arranged in a crescent parallel to the disto-lateral edges. Terminal diaphragms (Fig. 271) may be developed at a level beneath the apertural shelf. Intramural autozooids may have opercula substantially smaller than primary autozooids, closing beneath the level of the apertural shelf.

Eleozooids observed only as intramural buds within autozooids. Apertures small, longitudinally elongate, almost 1·5 × longer than wide, prominent, set in an oblique plane and directed proximally. Opercula observed in-situ.

Kenozooids rare.

Gonozooids unknown.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10429)

frontal length:	mean = 0·55 mm; SD = 0·059 mm; CV = 10·8; range = 0·47–0·63 mm
frontal width:	mean = 0·26 mm; SD = 0·010 mm; CV = 3·9; range = 0·24–0·27 mm
apertural length:	mean = 0·18 mm; SD = 0·005 mm; CV = 2·6; range = 0·18–0·20 mm
apertural width:	mean = 0·17 mm; SD = 0·007 mm; CV = 4·3; range = 0·17–0·18 mm

eleozooids (intramural)

apertural length:	*ca* 0·15 mm
apertural width:	*ca* 0·11 mm

REMARKS. Only a single specimen of this species is known, a free, unilamellar fragment measuring 8 × 5 mm. The presence of incipient intramural buds indicates that multilamellar growth was possible. *Reptomultelea reedi* most closely resembles the Lower Cenomanian Westfalian species *R. goldfussi* sp. nov. (see p. 73), especially in the well-rounded autozooidal apertures which indent distal zooids, but *R. reedi* has smaller zooids and opercula with pseudopores arranged in a crescent and not all over the surface as in *R. goldfussi*. A further difference between the two species is the presence of intramural eleozooids in *R. reedi*. Well-preserved eleozooidal apertures have not been studied, but the general shape of the opercula suggests that the eleozooids might be of the trifoliozooid-type.

Numerous small borings, probably circular but usually enlarged by chipping of the edges, penetrate the upper surface of this specimen (Fig. 269). Most occur in autozooidal opercula, but some are in terminal diaphragms or frontal walls. They resemble inferred predator borings described from other melicerititid species (Taylor, 1982).

DISTRIBUTION. Upper Cenomanian of Sarthe, France.

Reptomultelea reussi (Pergens, 1890) Figs 275–280

1872	*Diastopora oceani* d'Orbigny; Reuss: 110 (partim), pl. 27, fig. 3 [non fig. 2 = *Reptomultelea sarthacensis* (d'Orbigny)].
1890	*Semielea reussi* Pergens: 399.
?1892	*Semielea reussi* Pergens; Pergens: 278, pl. 11, fig. 7.
1899	*Reptomultelea*? *reussi* (Pergens); Gregory: 323.
1906	*Reptomultelea reussi* (Pergens); Lang: 63, fig. 10.

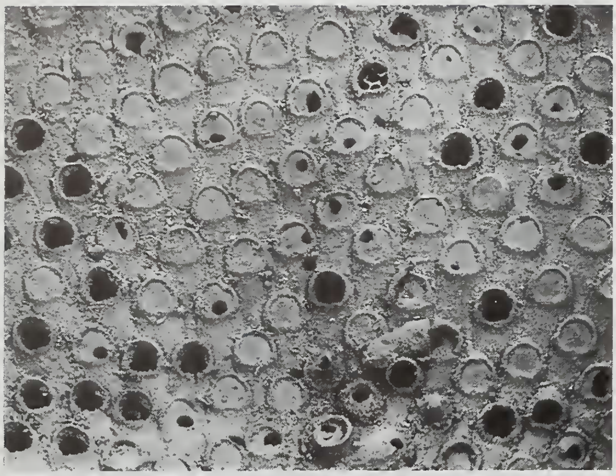
MATERIAL. Lectotype (selected herein): SMD un-numbered, the specimen figured by Reuss (1872: pl. 27, fig. 3) (Voigt photocard 2166), Cenomanian [*plenus* Zone], Dresden-Plauen, Germany.

Other material: BMNH D36115, Cenomanian, Untere Planer, Plauen, Dresden, Germany, Pergens Collection. VH 10428, 10433, Cenomanian, *plenus* Zone, Hoher Stein, Dresden-Plauen, Germany.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 277), each layer about 0·3 mm thick, sometimes cavariiform (Fig. 280) or with layers growing freely of the substratum. Ancestrula, overgrowth origins and pseudoancestrulae not observed. Organization fixed-walled. Zooidal aperture arrangement variable, often rather irregular.

Autozooids (Figs 275, 276) of medium size, frontally elongate, about twice as long as wide, hexagonal, pentagonal or diamond-shaped in outline with a pointed distal end; frontal wall occupying more than half of the frontal surface, slightly convex, with circular pseudopores; boundary wall salient, sometimes poorly developed. Aperture (Fig. 279) of moderate size, about 1·2–1·3 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width between hinge line and mid-length; apertural rim raised, more prominent distally; apertural shelf absent; hinge line gently bowed, teeth and bar not observed. Operculum rarely preserved in-situ, surface flat; pseudopores arranged in a crescent. Intramurally budded eleozooids may occur. Diaphragms not seen.

Kenozooids possibly present.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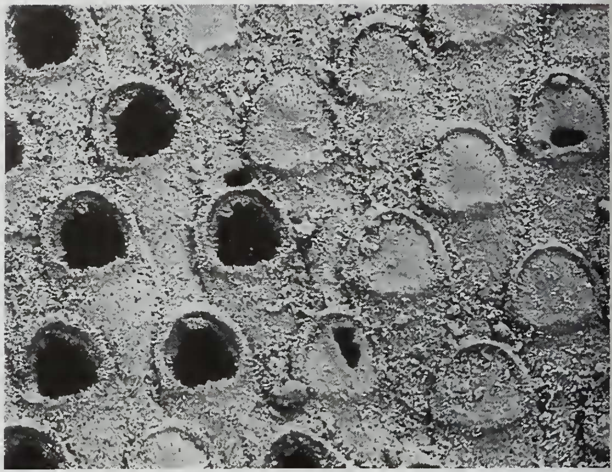
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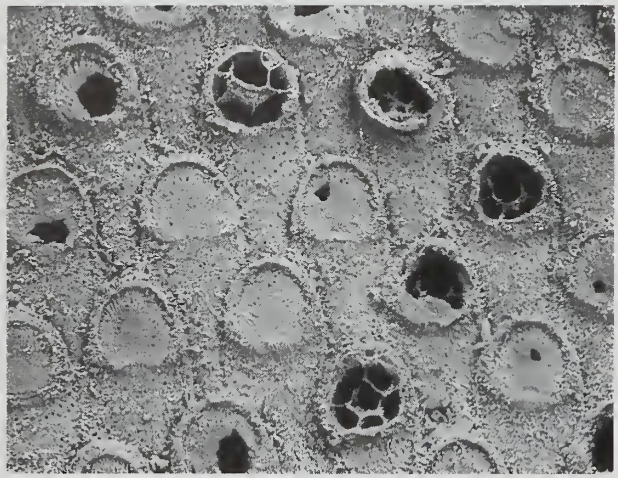
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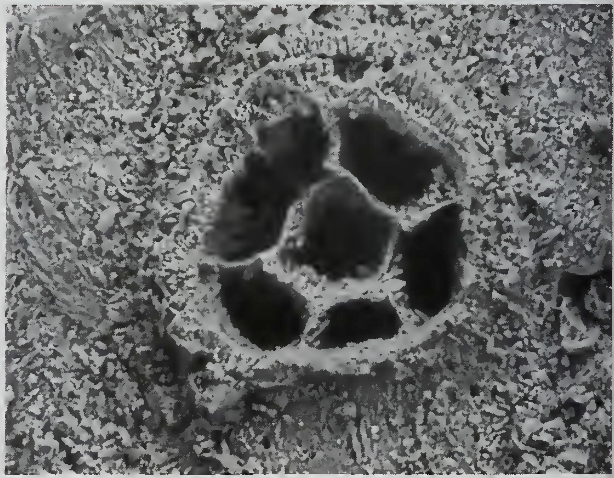
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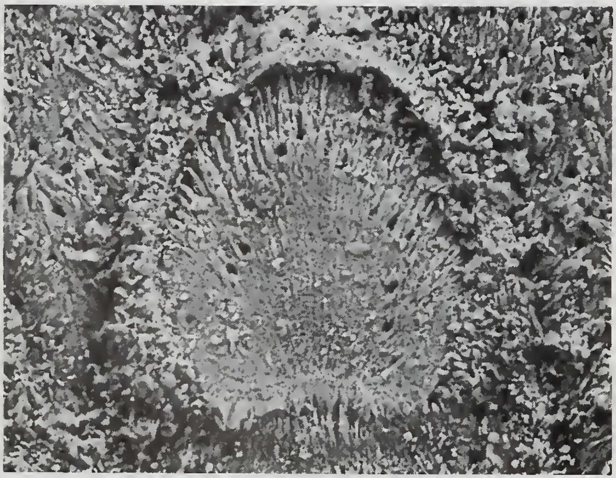
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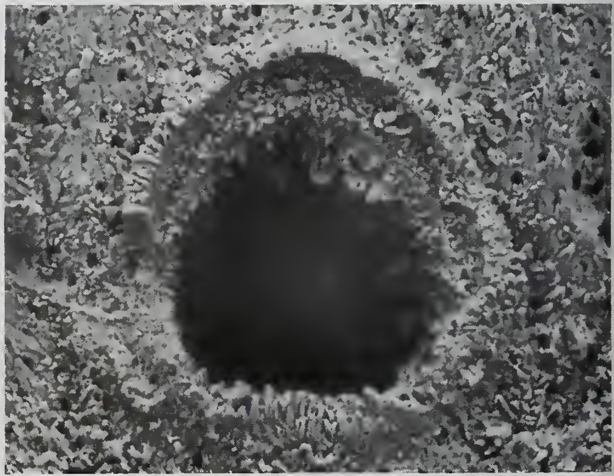
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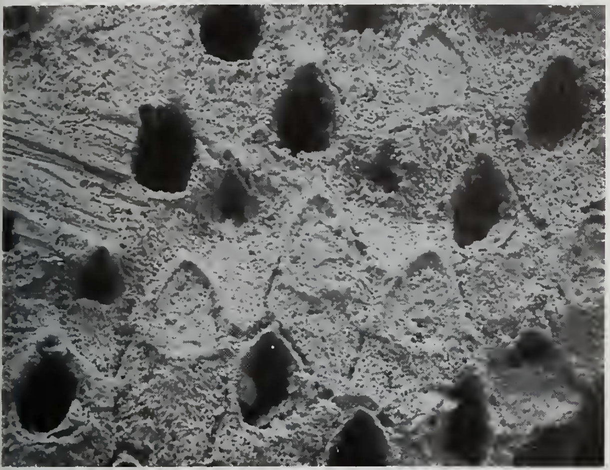
Figs 269–274 *Reptomultelea reedi* sp. nov., VH 10429, holotype, Upper Cenomanian, St Calais, Sarthe, France; 269, autozooids, some with bored opercula, × 22; 270, operculate and non-operculate autozooids, × 55; 271, autozooids variously with opercula, intrazooecial fissions and a terminal diaphragm (top left), × 55; 272, autozooidal aperture with intrazooecial fission, × 225; 273, autozooidal operculum, × 265; 274, autozooidal aperture, × 265.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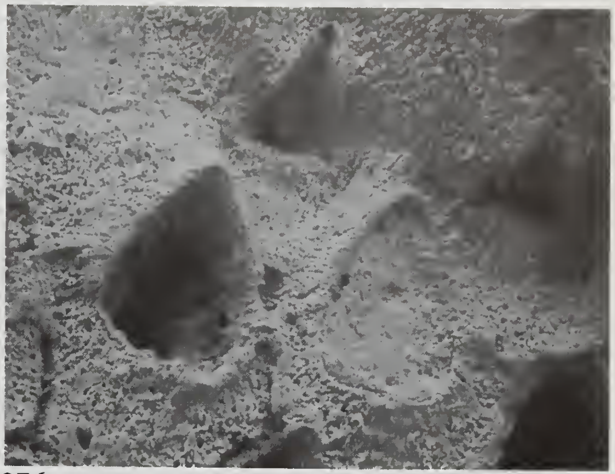
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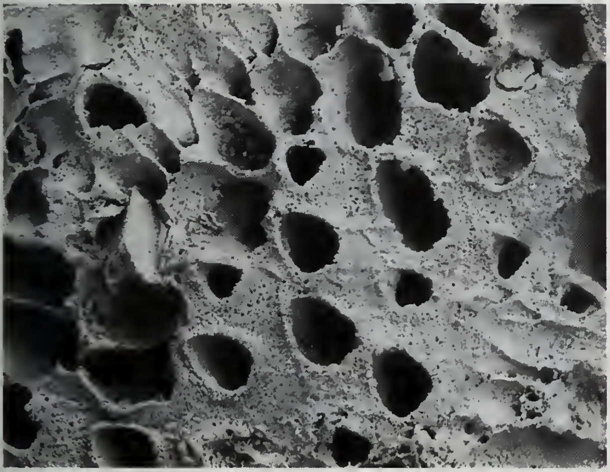
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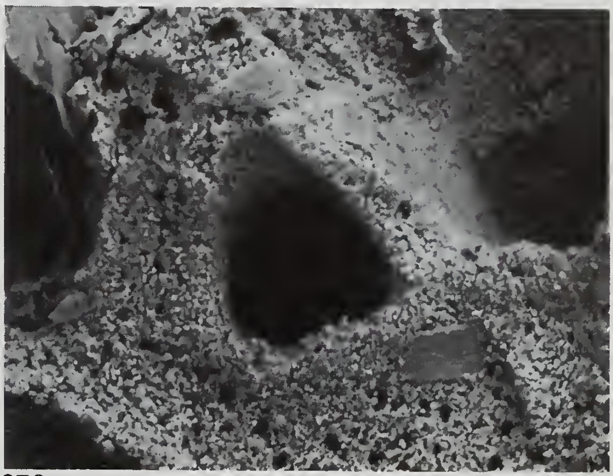
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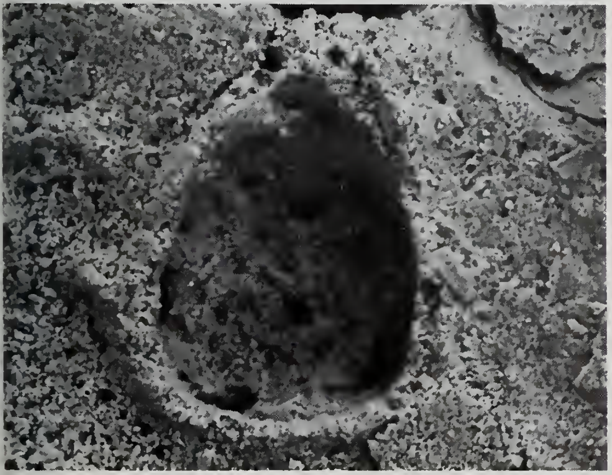
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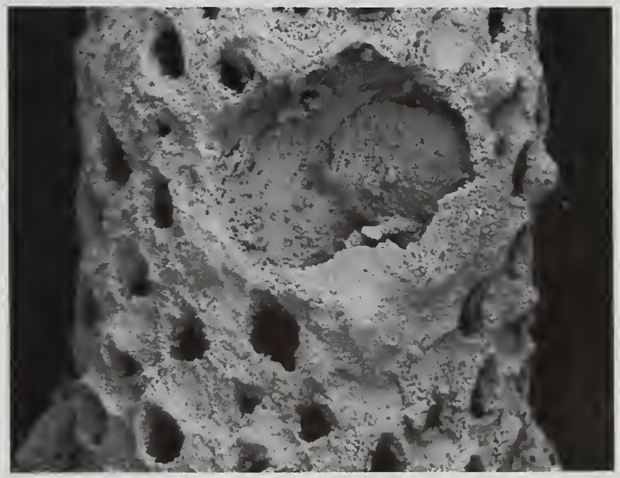
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Figs 275–280 *Reptomultelea reussi* (Pergens, 1890). 275, 276, BMNH D36115, Cenomanian, Untere Planer, Plauen, Dresden, Germany; 275, autozooids and eleozooids, × 50; 276, autozooids with and without opercula and an eleozooid above, × 105. 277–279, VH 10428 Cenomanian, *plenus* Zone, Hoher Stein, Dresden-Plauen, Germany; 277, abraded growing edge, × 50; 278, eleozooidal aperture, × 240; 279, autozooidal aperture, × 240. 280, VH 10433, Cenomanian, *plenus* Zone, Hoher Stein, cavariiform colony with worn gonozooid, × 50.

Eleozooids (Figs 275, 276) abundant, scattered or clustered; small, frontal surface variable in size, usually significantly shorter and narrower than autozooids, and almost twice as long as wide; frontal wall occupying more than half of frontal surface, often somewhat depressed. Aperture (Fig. 278) equidimensional to more than 1·5 × longer than wide, variable in size, smaller than an autozooidal aperture, attaining maximum width between hinge line and mid-length, distally elevated and pointed often with concave margins where prolonged by rostral shelf; apertural shelf lacking; apertural rim raised, especially distally; hinge line apparently with short median bar. Operculum rarely preserved in-situ, flat, conspicuously depressed beneath level of apertural rim. Intramurally budded eleozooids within host eleozooids not observed.

Gonozooids represented by a single, poorly-preserved example (Fig. 280). Frontally a little longer than wide, distal dilated frontal wall rounded subtriangular in shape. Ooeciopore destroyed.

MEASUREMENTS.
autozooids (10 zooids from VH 10428)
frontal length: mean = 0·53 mm; SD = 0·034 mm; CV = 6·4; range = 0·48–0·60 mm
frontal width: mean = 0·27 mm; SD = 0·024 mm; CV = 8·9; range = 0·24–0·32 mm
apertural length: mean = 0·20 mm; SD = 0·011 mm; CV = 5·2; range = 0·20–0·23 mm
apertural width: mean = 0·16 mm; SD = 0·010 mm; CV = 6·3; range = 0·15–0·18 mm

eleozooids (10 zooids from VH 10428)
frontal length: mean = 0·39 mm; SD = 0·085 mm; CV = 21·9; range = 0·30–0·57 mm
frontal width: mean = 0·21 mm; SD = 0·027 mm; CV = 12·9; range = 0·17–0·26 mm
apertural length: mean = 0·13 mm; SD = 0·041 mm; CV = 31·5; range = 0·08–0·20 mm
apertural width: mean = 0·10 mm; SD = 0·017 mm; CV = 16·7; range = 0·08–0·12 mm

gonozooids (1 zooid from VH 10433)
frontal length: *ca* 1·26 mm
distal frontal wall length: *ca* 1·10 mm
frontal width: *ca* 1·05 mm

REMARKS. Pergens (1890) proposed *Semielea reussi* as a new species to replace *Diastopora oceani* d'Orbigny *sensu* Reuss, 1872. His brief description is given only as a footnote to a revision of the Cretaceous cyclostomes figured by d'Orbigny (1851–54) in the 'Terrains Crétacés' and lacks any figures or mention of particular specimens. There is no evidence that he had any of his own material at hand when erecting this species. Therefore, the original specimens described by Reuss (1872) are taken as the syntypes of Pergens' new species. Unfortunately, the two figured syntypes of *S. reussi* (Reuss 1872: pl. 27, figs 2 and 3) are different species: the specimen shown in figure 2 (Voigt photocard 2814) is probably conspecific with *Reptomultelea sarthacensis* (d'Orbigny) (see p. 54); that shown in figure 3 (Voigt photocard 2166) is here chosen as the lectotype of *Reptomultelea reussi* (Pergens, 1890).

Pergens (1892) later provided a more complete description of *Semielea reussi* accompanied by a figure which shows a large eleozooid unlike those present in the lectotype of *S. reussi* but resembling the eleozooids of *R. sarthacensis*. This figure may be of a specimen, encrusting a sponge, from the Maastricht Museum which was on loan to Prof. E. Voigt when I had the opportunity to examine it in November 1987. This specimen is conspecific with *R. sarthacensis*. Two identified specimens of *S. reussi* were donated to the BMNH by Pergens and are registered as D36115 and D36116. The first is conspecific with the lectotype of *S. reussi*, whereas the second is indeterminate. It seems likely, therefore, that Pergens' concept of *S. reussi* was a broad one which included *R. sarthacensis* as well as *R. reussi*.

Reptomultelea reussi is readily distinguished by its small eleozooids with apertures of a similar shape to the autozooid apertures, except that they are prolonged distally by the presence of a short rostral shelf. Categorizing these eleozooids according to the tripartite classification of Taylor (1986*a*) is difficult; they are too small to be rostrozooids, lack the inverted T-shape of trifoliozooids, and are more pointed than demizooids. Perhaps they are best regarded as highly reduced rostrozooids.

None of the available material of *Reptomultelea reussi* is well-preserved; all specimens are variably abraded and have cement-obscured surfaces. Poor preservation partly explains the high variance of the eleozooidal dimensions, but a good deal of this variability is biological in origin.

Both the lectotype colony and specimen VH 10433 (Fig. 280) are cavariiform, thereby explaining Pergens' (1890, 1892) placement of the species in *Semielea* (see p. 42). Other specimens do not have such hollow growth-forms and assignment of the species to *Semielea* is therefore unjustified.

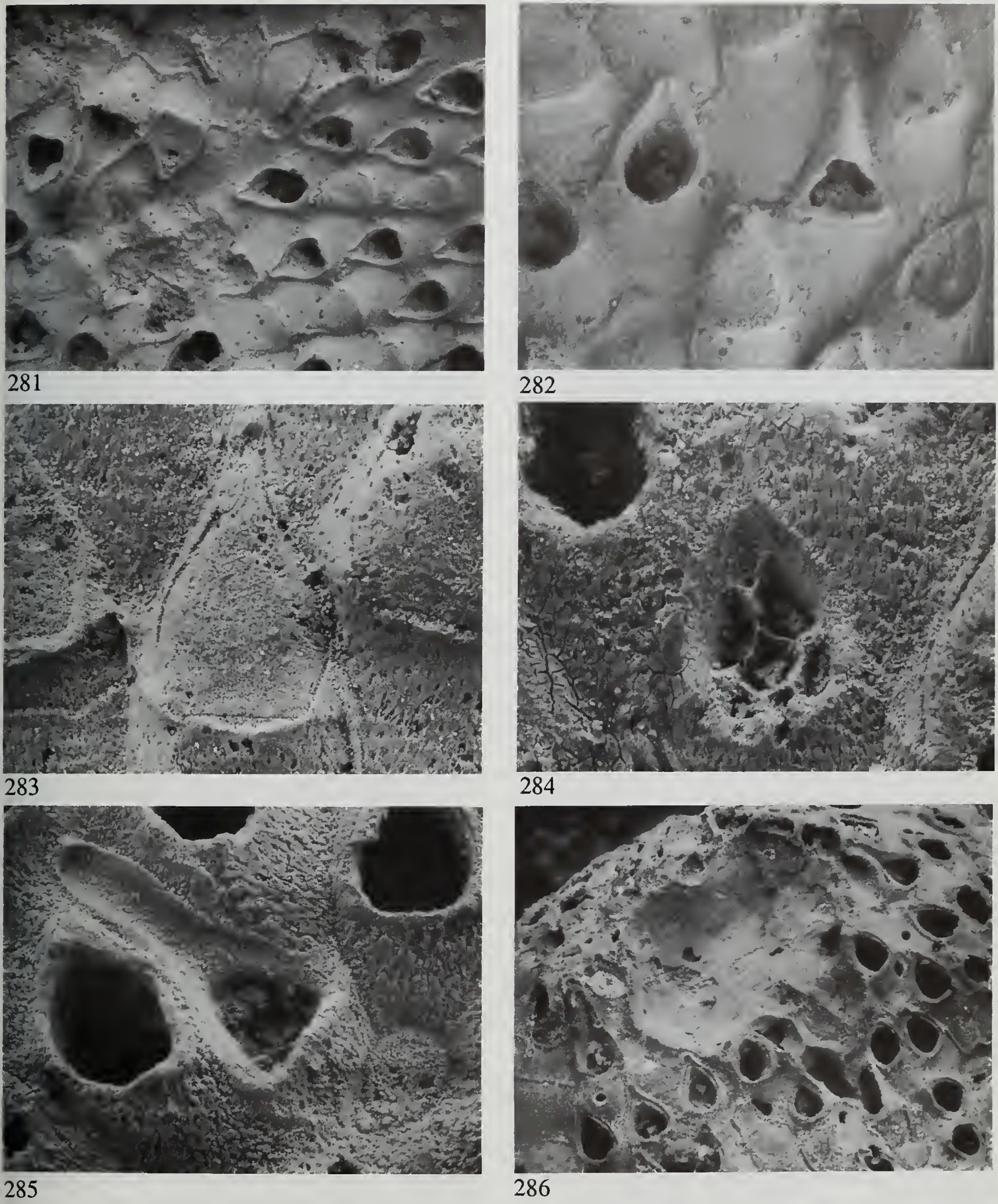
DISTRIBUTION. Upper Cenomanian (*plenus* Zone) of Dresden, Germany.

Reptomultelea sarissata Gregory, 1899 Figs 281–286

1899 *Reptomultelea sarissata* Gregory: 322, pl. 16, fig. 7.
1906 *Reptomultelea sarissata* Gregory; Lang: 63, fig. 9.
1912 *Meliceritites sarissata* (Gregory); Levinsen: 40, pl. 2, figs 1–3.

MATERIAL. Holotype: BMNH D7106 (main specimen plus two fragments), Upper Chalk, Beachy Head, Sussex, Gregory Colln.

Other material: BMNH D8011 (main specimen plus two fragments), D8012, [Coniacian], *cortestudinarium* Zone, Seaford, Sussex, Brydone Colln. BMNH D8568, D8576, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, Gamble Colln. BMNH D11020, D11224, [?Coniacian], top of *cortestudinarium* Zone or base of *coranguinum* Zone, Chatham, Kent, Gamble Colln. BMNH D26835–9, D27022–4, [Coniacian], *cortestudinarium* Zone, Worms Heath, Surrey. BMNH D43661–2, [Coniacian], *cortestudinarium* Zone, Seaford Head, Sussex, Rowe Colln. BMNH D46891, Upper Chalk, Seaford, Sussex, Stuart Colln. BMNH D59276, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, Rowe Colln. BMNH D58929 (7 fragments), Coniacian/Santonian, *decipiens* Zone Chalk, Vattetot-sur-mer, Seine-Maritime, France, Taylor & Hammond Colln. ZMC M35, Chalk, 'Chatham or Luton', Gamble Colln (specimen, on a flint, figd by Levinsen, 1912: pl. 2, figs 1–3). VH un-numbered: Coniacian, Fécamp, Seine-Maritime, France; Coniacian, Vattetot-sur-mer, Seine Maritime, France.



Figs 281–286 *Reptomultelea sarissata* Gregory, 1899. 281–282, BMNH D46891, Upper Chalk, Seaford, Sussex, 281, area of coalescent growth with autozooids, kenozooids and eleozooids, × 20; 282, autozooids and eleozooid with a broken operculum, × 48. 283–285, BMNH D7106, holotype, Upper Chalk, Beachy Head, Sussex; 283, autozooidal operculum, × 105; 284, autozooidal aperture showing intrazooecial fission, × 95; 285, eleozooid budded from a pseudoancestrula (lower right), × 77. 286, BMNH D8568, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, crushed gonozooid, × 23.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·35 mm thick, layers sometimes growing freely with an exposed basal lamina. Overgrowths originate through intrazooecial fission (Fig. 284); pseudoancestrula an autozooid with aperture about 0·21 mm long by 0·17 mm wide; peri-pseudoancestrular buds may include autozooids, eleozooids (Fig. 285) or gonozooids, initiating secondary zone of astogenetic change during which apertural size increases and apertures become more pointed. Organization fixed-walled. Zooidal apertures arranged in quincunx except where disrupted near overgrowth origins and anastomoses.

Autozooids (Figs 281–282) very large, frontally elongate, generally 2–3 × longer than wide, hexagonal in outline, pointed distally; frontal wall convex, pseudopores slightly longitudinally elongate; boundary wall salient, often inconspicuous. Aperture (Fig. 284) of large size, longitudinally elongate, on average 1·6 × longer than wide, ogee arch-shaped with a short but distinct distal prolongation with concave sides, attaining maximum width between hinge line and mid-length; apertural rim salient; apertural shelf narrow, tapering proximally; hinge line with a median bar, teeth ?present. Operculum (Fig. 283) often preserved in-situ, convex; pseudopores not visible, probably as a result of poor preservation. Terminal diaphragms and intramural buds not observed.

Kenozooids occasionally present, usually located at overgrowth anastomoses (Fig. 281).

Eleozooids (Figs 281, 285) common; frontally very large, elongate, 2–3 × longer than wide, longer and generally a little wider than the autozooids. Aperture elongate, widest proximally at level of hinge line, narrowing with appearance of rostral shelf to become parallel-sided or very slightly spatulate, rounded and depressed distally. Opercula sometimes preserved in-situ, convex, pseudopores not visible, probably as a result of poor preservation. Intramurally budded eleozooids observed; apertures shorter than those of host eleozooid and less depressed distally.

Gonozooids (Fig. 286) represented by a single, broken example budded from a pseudoancestrula. Frontally pear-shaped, dilated frontal wall about 1·3 × longer than wide. Proximal floor showing outlines of underlying zooids, distal wall smooth. Ooeciopore damaged in available material. Atrial ring present.

MEASUREMENTS.
autozooids (10 zooids from holotype BMNH D7106)
frontal length: mean = 0·92 mm; SD = 0·134 mm; CV = 14·6; range = 0·78–1·11 mm
frontal width: mean = 0·38 mm; SD = 0·038 mm; CV = 10·2; range = 0·30–0·44 mm
apertural length: mean = 0·40 mm; SD = 0·020 mm; CV = 5·0; range = 0·36–0·44 mm
apertural width: mean = 0·24 mm; SD = 0·014 mm; CV = 5·7; range = 0·23–0·27 mm

eleozooids
(3 zooids from holotype BMNH D7106)
frontal length: range = 1·32–1·44 mm
frontal width: range = 0·48–0·51 mm
apertural length: range = 0·72–0·83 mm
apertural width: range = 0·32–0·36 mm

(7 zooids from BMNH D8011)
frontal length: mean = 1·16 mm; SD = 0·040 mm; CV = 3·4; range = 1·13–1·22 mm
frontal width: mean = 0·45 mm; SD = 0·039 mm; CV = 8·8; range = 0·41–0·51 mm
apertural length: mean = 0·73 mm; SD = 0·031 mm; CV = 4·3; range = 0·69–0·78 mm
apertural width: mean = 0·33 mm; SD = 0·013 mm; CV = 4·1; range = 0·32–0·35 mm

gonozooids (1 zooid from BMNH D8568)
frontal length: 2·13 mm
distal frontal wall length: 1·97 mm
frontal width: 1·61 mm
ooeciopore width: *ca* 0·15 mm (broken)

REMARKS. *Reptomultelea sarissata* is a very distinctive species readily recognized by the large, ogee arch-shaped autozooidal apertures. Eleozooidal morphology suggests affinities with *R. dixoni* (Lang) (see p. 69), which also has large autozooids. *R. sarissata* probably has a stratigraphical range restricted to the Coniacian (*cortestudinarium* Zone and equivalents).

Like other species of *Reptomultelea* from chalk facies, colonies are generally nodular to lamellar in shape and often appear to have been attached to soft-bodied organisms whose traces may remain as poorly-defined bioimmurations on the undersides of colonies.

DISTRIBUTION. Coniacian (?basal Santonian) of southern England and northern France.

Reptomultelea scanica sp. nov. Figs 287–296

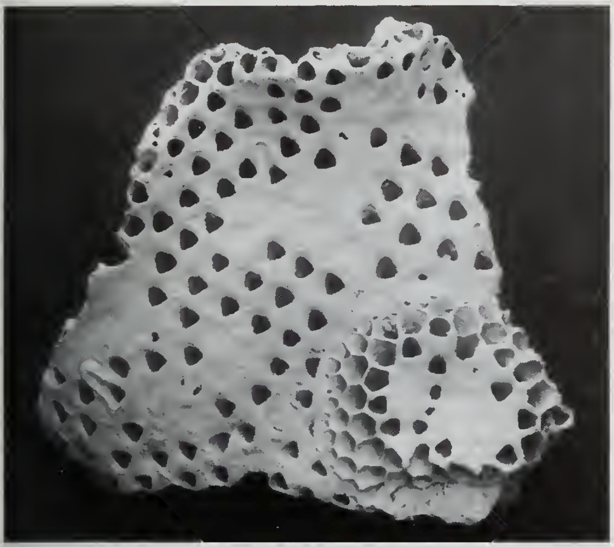
MATERIAL. Holotype: VH 10441, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. Paratype: VH 10442, 10549 (sample), same details as holotype.

NAME. After the provenance.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 290), each layer about 0·3 mm thick, usually with a transversely undulose basal lamina growing freely of the substratum. Overgrowths originate by intrazooecial fission; pseudoancestrula an autozooid, aperture about 0·10 mm wide; periancestrular buds commence a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. apertures arranged in approximate quincunx away from overgrowth origins and anastomoses. Mural spines visible in proximal parts of zooids exposed on fractured edges of specimens.

Ancestrula, probably of this species (Fig. 288), fouling the basal lamina of VH 10442, short (length 0·48 mm) with large protoecium (width 0·38 mm), negligable distal ancestrular tube, and aperture 0·15 mm long by 0·14 mm wide. Operculum not preserved, although presence of a straight hinge line implies that ancestrula was originally operculate.

Autozooids (Figs 289) small, frontally elongate, usually less than twice as long as wide and subrhomboidal in outline shape, rounded distally; frontal wall slightly convex, pseudopores subcircular; boundary wall salient but inconspicuous and mainly comprising apertural rims. Aperture (Fig. 291) of moderate size, occupying about half of the frontal area, longitudinally elongate, 1·1–1·3 × longer than wide, rounded distally, attaining maximum width between the hinge line and mid-length; apertural rim often thickened at proximolateral corners of aperture; hinge line with short median bar between low (?)teeth; apertural shelf broad



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288

Figs 287–288 *Reptomultelea scanica* sp. nov., Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. 287, VH 10441, holotype, colony fragment with newly-developed overgrowth (lower right), × 17. 288, VH 10442, ancestrula (presumed to be of this species) fouling underside of main colony, × 88.

distally, tapering proximally and disappearing at about the level of maximum aperture width. Operculum (Fig. 293) often preserved in-situ, convex; pseudopores radially elongate, scattered all over surface of operculum. Terminal diaphragms (Fig. 294) observed just proximal of apertural shelf, apparently lacking pseudopores. Intramurally budded autozooids probably represented by zooids with smaller opercula and thicker apertural rims.

Kenozooids rare, sometimes developed immediately distal of eleozooids.

Eleozooids (Figs 289, 295) moderately common, scattered, frontally elongate, about 2·5 × longer than wide, longer and wider than the autozooids, well-rounded distally. Aperture longitudinally elongate, generally 2·5 × longer than wide, distally parallel-sided or slightly spatulate and rounded; rostrum forming an extensive platform; apertural rim raised. Opercula not observed in-situ. Intramural buds and terminal diaphragms unknown.

Gonozooids known from a single example (Fig. 296). Frontally elongate, twice as long as wide, a short parallel-sided tube emerging from the maternal aperture and dilating into a longitudinally ovoidal shape. Autozooids adjacent to distal part of gonozooid are orientated parallel to margins of gonozooid. Ooeciopore transversely elliptical, twice as wide as long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10441)

frontal length:	mean = 0·44 mm; SD = 0·023 mm; CV = 5·5; range = 0·39–0·47 mm
frontal width:	mean = 0·24 mm; SD = 0·014 mm; CV = 5·9; range = 0·23–0·26 mm
apertural length:	mean = 0·20 mm; SD = 0·006 mm; CV = 3·2; range = 0·20–0·21 mm
apertural width:	mean = 0·17 mm; SD = 0·009 mm; CV = 5·6; range = 0·15–0·18 mm

eleozooids (3 zooids from holotype VH 10441 and 3 zooids from VH 10442)

frontal length:	mean = 0·76 mm; SD = 0·080 mm; CV = 10·5; range = 0·65–0·87 mm
frontal width:	mean = 0·30 mm; SD = 0·013 mm; CV = 4·5; range = 0·29–0·32 mm
apertural length:	mean = 0·44 mm; SD = 0·048 mm; CV = 10·9; range = 0·39–0·50 mm
apertural width:	mean = 0·18 mm; SD = 0·011 mm; CV = 6·2; range = 0·17–0·20 mm

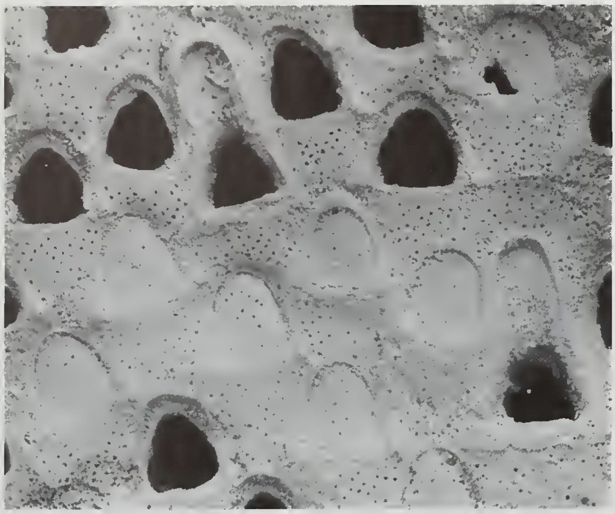
gonozooids (1 zooid from VH 10442)

frontal length:	1·80 mm
distal frontal wall length:	1·64 mm
frontal width:	0·90 mm
ooeciopore length:	0·09 mm
ooeciopore width:	0·18 mm

REMARKS. The youngest known species of *Reptomultelea*, *R. scanica* is characterized by its spatulate eleozooids, high autozooidal apertures which occupy about half of the frontal area of the zooid, and pseudopores distributed across the entire surface of the autozooidal opercula. Eleozooid shape is similar to *R. filiozati* (Levinsen), while the distribution of opercular pseudopores is reminiscent of *R. goldfussi* sp. nov., but other characters ensure that neither of these species could be confused with *R. scanica*.

Available specimens are small fragments of larger colonies. With the exception of one specimen which encrusts a shell fragment (?brachiopod), original substrates are not preserved and the basal lamina evidently grew freely into space. The shell-encrusting colony shows the beginnings of cavariiform growth.

DISTRIBUTION. Lower Campanian of Scania, Sweden.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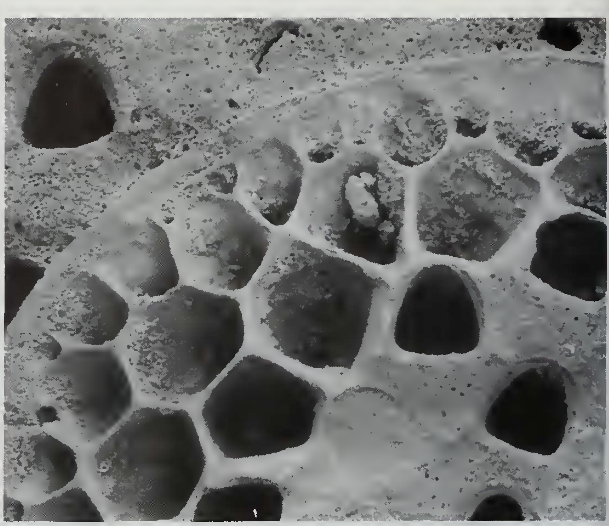
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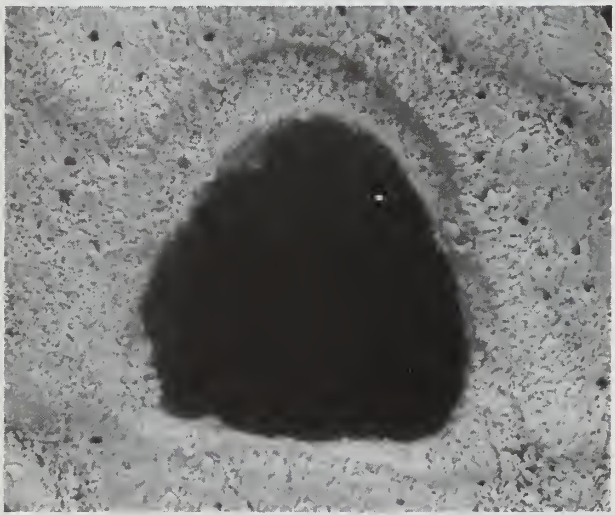
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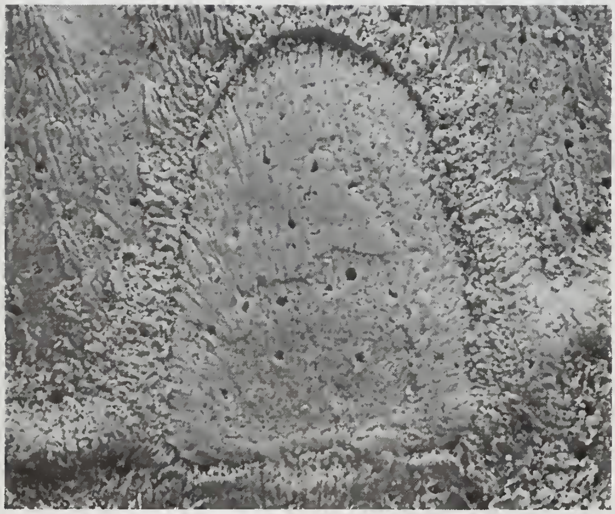
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294

Figs 289–294 *Reptomultelea scanica* sp. nov., Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. 289–291, VH 10441, holotype; 289, autozooids and two eleozooids, × 67; 290, growing edge of overgrowth, × 74; 291, autozooidal aperture, × 270. 292–294, VH 10442; 292, ooeciopore, × 130; 293, autozooidal operculum, × 275; 294, autozooidal aperture with terminal diaphragm, × 270.

Fig. 295 *Reptomultelea scanica* sp. nov., VH 10441, holotype, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden, eleozooid, × 135.

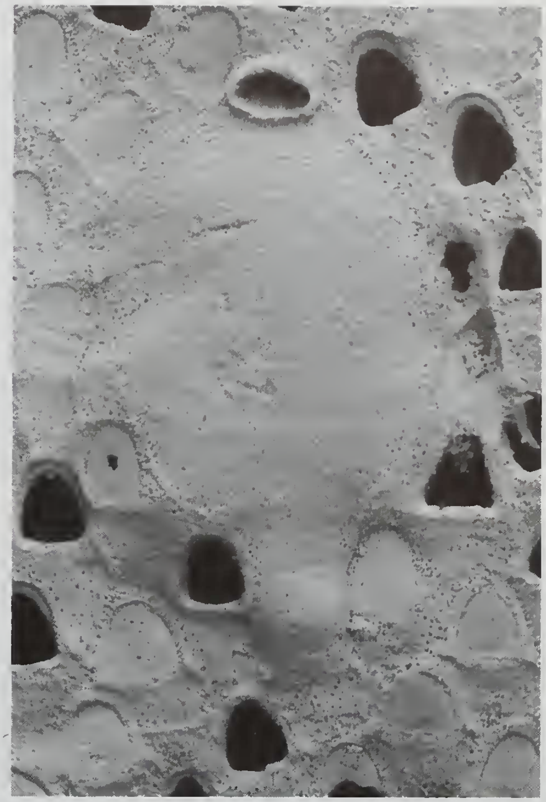


Fig. 296 *Reptomultelea scanica* sp. nov., VH 10442, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden, gonozooid, × 58.

Reptomultelea tuberculata (d'Orbigny, 1853)
Figs 297–302

1853 *Clausimultelea tuberculata* d'Orbigny: 656, pl. 784, figs 12–15.
1890 *Clausimultelea tuberculata* d'Orbigny; Pergens: 398.
1899 *Clausimultelea tuberculata* d'Orbigny; Gregory: 405.
1912 *Meliceritites tuberculata* (d'Orbigny); Levinsen: 35, pl. 6, figs 1–3.

MATERIAL. Holotype: MNHN d'Orbigny Collection 8203 (Voigt photocard 3717), Senonian, Triquerville, Seine-Inférieure, France.

Other material: BMNH D54295, Santonian, Evreux, Eure, France, Voigt Colln. VH un-numbered material: Coniacian, Fécamp; Coniacian, Vattetot-sur-Mer; Santonian, Evreux; Santonian (*coranguinum* Zone), Aulnay-sur-Iton.

DESCRIPTION. Colony multilamellar, each layer about 0·3 mm thick, growing as a series of discoidal subcolonies. Overgrowths originate through intrazooecial fission; pseudoancestrulae are autozooids and are followed by a secondary zone of astogenetic change. Organization fixed-walled. Zooidal apertures variably arranged.

Autozooids (Fig. 297) of medium size, frontally elongate, on average a little less than twice as long as wide, often hexagonal in outline with distal margin prolonged by the aperture; boundary wall salient. Aperture (Fig. 299) of moderate size, very tall, 1·5 × longer than wide, attaining maximum width between the hinge line and mid-length, rounded distally; apertural rim raised; apertural shelf moderately wide, tapering proximally; hinge line with a median bar and ?teeth. Operculum (Fig. 298) convex; pseudopores number about 18 arranged in a crescent. Terminal diaphragms not observed. Intramurally budded eleozooids (Fig. 300) present within many autozooids; aperture similar in shape but shorter than those of primary eleozooids, a little raised distally, an area of calcification intervening between hinge line of host zooid and proximal edge of eleozooid aperture; operculum not observed.

Kenozooids (Figs 297, 301) numerous, intercalated between the other zooids and sometimes completely surrounding them.

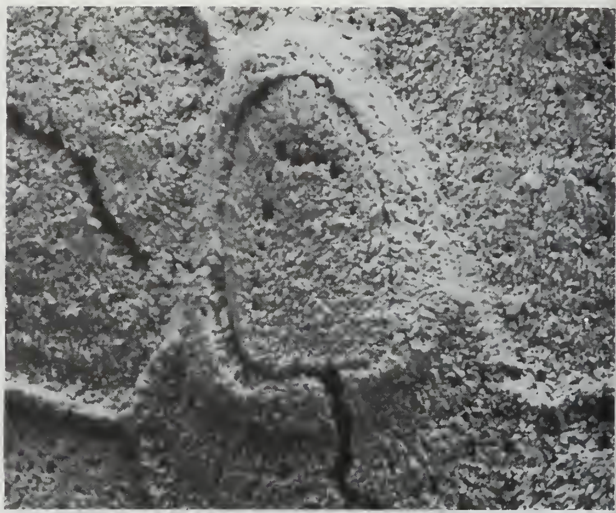
Eleozooids (Figs 297, 301) common, elongate, about twice as long as wide, a little longer and narrower than the autozooids, distal outline narrow where prolonged by aperture. Aperture (Fig. 302) elongate, narrow, about 3 × longer than wide, attaining maximum width at the level of the hinge line, slightly indented laterally by rostral shelf between hinge line and mid-length, distally pointed and slightly raised. Opercula not observed in-situ. Intramural buds not seen within eleozooids.

Gonozooids unknown.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from BMNH D54295)

frontal length:	mean = 0·54 mm; SD = 0·046 mm; CV = 8·6; range = 0·47–0·65 mm


297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Figs 297–302 *Reptomultelea tuberculata* (d'Orbigny, 1853), BMNH D54295, Santonian, Evreux, Eure, France; 297, autozooids, eleozooids and kenozooids, × 60; 298, autozooidal operculum, × 225; 299, autozooidal aperture, × 225; 300, two intramural eleozooids, × 140; 301, eleozooid surrounded by operculate autozooids and kenozooids, × 105; 302, eleozooidal aperture, × 240.

Frontal width: mean = 0·29 mm; SD = 0·023 mm; CV = 7·8; range = 0·24–0·32 mm
apertural length: mean = 0·21 mm; SD = 0·010 mm; CV = 4·7; range = 0·20–0·23 mm
apertural width: mean = 0·14 mm; SD = 0·011 mm; CV = 7·4; range = 0·12–0·15 mm

Eleozooids (4 zooids from BMNH D54295)
Frontal length: range = 0·54–0·65 mm
Frontal width: range = 0·26–0·30 mm
apertural length: range = 0·18–0·26 mm
apertural width: range = 0·08 mm

REMARKS. *Clausimultelea tuberculata* d'Orbigny, 1853 is the ype species by monotypy of *Clausimultelea* d'Orbigny, 1853, a genus here placed in synonymy with *Reptomultelea* (see p. 46). The narrow, acuminate apertures of the eleozooids, numerous kenozooids and high autozooidal apertures are useful features in identification of the species. The eleozooids nvite comparison with *Meliceritites gothica* and similar species; a functional, if not phylogenetic, connection seems possible.

The only specimen of *Reptomultelea tuberculata* in the d'Orbigny Collection is a large colony reaching 50 mm in diameter and preserved on the outside of a flint. This specimen has been labelled 'Type' by E. Voigt and corresponds well with d'Orbigny's plate 784, fig. 12. Levinsen's 1912) material of *R. tuberculata* could not be positively dentified among his collection of melicerititids in the ZMC, although this collection does include a specimen from Fécamp labelled '*Clausimultelea* n. sp.'. The record of *R. uberculata* given by Levinsen (p. 36) from the Danian of the Paris Basin is highly doubtful as the genus *Reptomultelea* is not known to range above the Campanian.

DISTRIBUTION. Coniacian to Santonian of France.

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